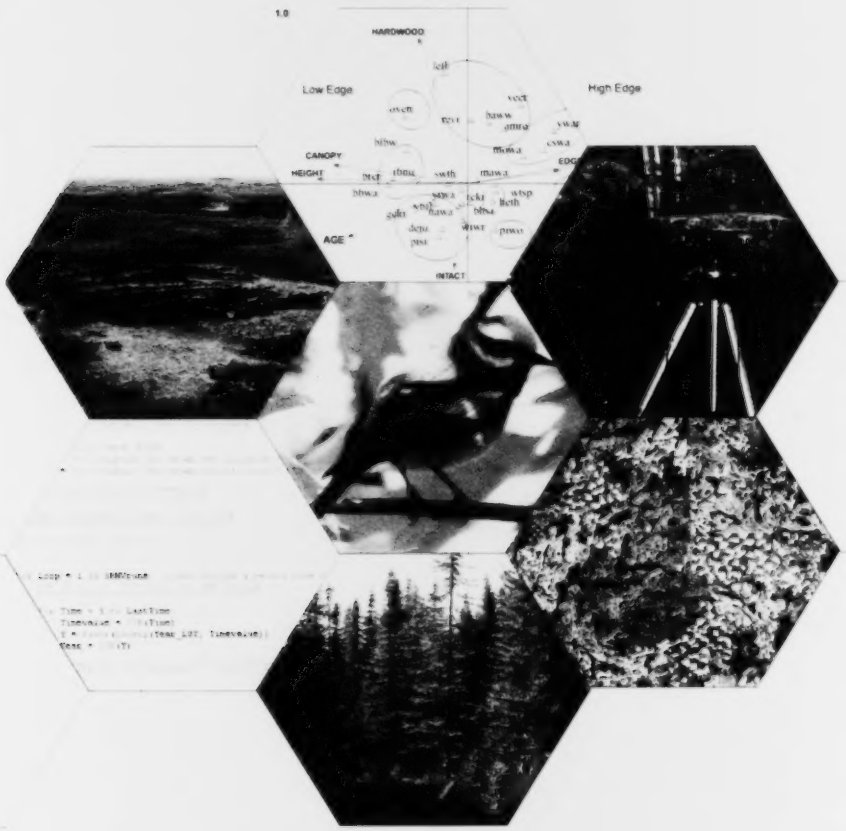
Centre for Northern Forest Ecosystem Research Technical Report 002

Forest Policy Scenario Analysis

Evaluating the Effectiveness of Coarse-Filter Policy Options on Conserving Forest Songbird Communities



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2008-01668/

Centre for Northern Forest Ecosystem Research ***Technical Report 002***

Forest Policy Scenario Analysis

Evaluating the Effectiveness of Coarse-Filter Policy Options on Conserving Forest Songbird Communities

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September 2007

(Centre for Northern Forest Ecosystem Research Technical Report 002)
Forest Policy Scenario Analysis: Evaluating the Effectiveness of Coarse-Filter Policy Options on Conserving Forest Songbird Communities.

Available in print: ISBN 978-1-4249-5174-1
Available also on the Internet (PDF): ISBN 978-1-4249-5175-8

Cette publication spécialisée n'est disponible qu'en anglais.

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Printed in Ontario, Canada

Single copies of this publication are available from:

Centre for Northern Forest Ecosystem Research
Ministry of Natural Resources
955 Oliver Road
Thunder Bay, ON
Canada P7B 5E1
Phone: (807) 343-4000
Fax: (807) 343-4001

Please cite as:

Rempel, R.S. J. Baker, P. C. Elkie, M. J. Gluck, J. Jackson, R. S. Kushneriuk, T. Moore, and A. H. Perera. 2007. Forest Policy Scenario Analysis: Evaluating the Effectiveness of Coarse-Filter Policy Options on Conserving Forest Songbird Communities. Technical Report CNFER TR-002. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada. 32pp.

FOREWARD

The information presented in this report has been published in the following two journal articles. Some sections of this report have been summarized to focus the information presented so that it would be more relevant and useful for forest management practitioners and policy makers. For more in depth descriptions of the methods and results please refer to the original articles, and cite these articles when referring to the research in scholarly papers.

Rempel, R. S., J. Baker, P. C. Elkie, M. J. Gluck, J. Jackson, R. S. Kushneriuk, T. Moore, and A. H. Perera. 2007. Forest policy scenario analysis: Sensitivity of songbird community to changes in forest cover amount and configuration. Avian Conservation and Ecology – Écologie et conservation des oiseaux 2(1): 5. [online] URL: http://www.ace-eco.org/vol2/iss1/art5/

Rempel, R. S. 2007. Selecting focal songbird species for biodiversity conservation assessment: response to forest cover amount and configuration. Avian Conservation and Ecology – Écologie et conservation des oiseaux 2(1): 5. [online] URL: http://www.ace-eco.org/vol2/iss1/art6/

EXECUTIVE SUMMARY

Changes in mature forest cover amount, composition and configuration can be of significant consequence to wildlife populations. The response of wildlife to forest patterns is of concern to forest managers because it lies at the heart of such competing approaches to forest planning as aggregated versus dispersed harvest block layouts. In this study we developed a species assessment framework to evaluate the outcomes of forest management scenarios on biodiversity conservation objectives.

In Part I of the report we describe the selection of focal species for creating an assessment framework, and illustrate how we use their habitat requirements to define the range of conditions that should be maintained on the landscape. Multivariate analysis and logistic regression were used to describe these relationships in more detail. Based on statistically defendable inferences and habitat model coefficients, 13 species were selected with habitat associations ranging from high to low edge density, homogeneous to heterogeneous forest matrix, hardwood to softwood dominated overstory, young to old stands, and open to closed canopy. We found that variations in mature forest cover amount and configuration had relatively little influence on the overall boreal forest songbird community, but that individual species differ in their response to these variables. To be successful, biodiversity conservation strategies must emulate the patterns created through natural disturbance by maintaining the full range of forest cover homogeneity and heterogeneity on the landscape. The habitat requirements for Alder Flycatcher, Black-and-white Warbler, Bay-breasted Warbler, Blackburnian Warbler, Brown Creeper, Common Yellowthroat, Chestnut-sided Warbler, Least Flycatcher, Ovenbird, Red-breasted Nuthatch, Red-eyed Vireo, Winter Wren and White-throated Sparrow describe a broad range of habitat conditions that at a minimum describe necessary coarse-filter conditions to sustain the boreal songbird community in Ontario. This suite of species can also serve in developing a "bioassay" to evaluate the effectiveness of forest policy to conserve biodiversity through emulation of natural disturbance.

In Part II of the report we discuss how scenarios were assessed in the context of a broad range of forest structure and pattern. This range in patterns would be expected to occur under natural disturbance and succession processes. The spatial habitat models were used to predict the effects of varying degrees of mature forest cover amount, composition and configuration on habitat occupancy for a set of 13 focal songbird species. We used a spatially-explicit harvest scheduling program to model forest management options and simulate future forest conditions resulting from alternative forest management scenarios,

and used a process-based fire-simulation model to simulate future forest conditions resulting from natural wildfire disturbance. Spatial pattern signatures were derived for both habitat occupancy and forest conditions, and these were placed in the context of the simulated range of natural variation. Strategic policy analyses were set in the context of current Ontario forest management policies. This included use of sequential time-restricted harvest blocks (created for Woodland caribou conservation) and delayed harvest areas (created for American marten conservation). This approach increased the realism of the analysis, but reduced the generality of interpretations.

In this study we found that to be successful, biodiversity conservation strategies must emulate the patterns created through natural disturbance by maintaining the full range of forest cover homogeneity and heterogeneity on the landscape. This variation in landscape pattern can be achieved by creating habitat conditions to support a range of focal species that collectively describe the wide range of niche-space occupied by the forest songbird community. The combination of community-level and species-level analyses help to identify the set of focal species that land managers should consider when developing forest management plans. Providing the habitat needs for all members within this focal group will ensure important "coarse-scale" habitat needs are not lost on the landscape. Defining the habitat needs for individual species within the focal group provides the basis of a concrete strategy for identifying appropriate levels and combinations of landscape patterns required to conserve biodiversity for a broad range of forest songbirds, and perhaps even the invertebrates and other food-web species associated with these birds. Future studies need to evaluate these predications at different times and places because habitat associations may be influenced by as yet unidentified causal factors (e.g., distributions in insect prey abundance). Although many of the local-scale habitat associations are relatively well known, most of the landscape-scale habitat associations are less well understood. Further study is required to evaluate the robustness of habitat associations at the broader landscape scales.

The results of this study support the adoption of boreal forest management strategies that create clustered areas of high edge separated by large areas of intact forest matrix. It is the combination of these conditions that will create the diversity of forest patterns necessary to support the full range of boreal forest songbirds. The analysis also supports using compositional targets based on natural disturbance simulations. At the community level, some songbird species are resilient to edge, and others less so. Only by creating the combination of conditions will the coarse-filter habitat needs of the entire community be met. Spatially explicit, quantitative habitat models developed for a focal set of songbird species describe the target levels and range of variability in forest conditions required, as a minimum, to support the full complement of boreal forest songbird species. The simulated range of natural variability helps define the temporal variability that should be expected for both forest variables and associated habitat occupancy patterns. The approach of strategically modelling long-term patterns, but using realistic operational constraints, adds both validity and complexity to model interpretation.

SOMMAIRE

Les changements dans l'étendue, la composition et la configuration du couvert forestier mature peuvent avoir des conséquences importantes sur les populations d'espèces sauvages. Les aménagistes forestiers s'intéressent aux réactions des espèces sauvages aux configurations de la forêt parce qu'elles se trouvent au cœur d'approches aussi concurrentes de l'aménagement forestier que les dispositions regroupée ou dispersée des parcelles de récolte. Dans cette étude, nous avons établi un cadre d'évaluation des espèces pour apprécier l'effet des scénarios d'aménagement forestier sur les objectifs de conservation de la biodiversité.

Dans la partie I du rapport, nous décrivons la sélection des espèces focales pour la création d'un cadre d'évaluation et nous indiquons comment nous utilisons leurs besoins en matière d'habitat pour définir

l'ensemble de conditions qui devraient être maintenues dans le paysage. Nous avons utilisé l'analyse multivariable et la régression logistique pour décrire ces relations plus en détail. En nous basant sur des inférences statistiques prouvables et des paramètres de modèles d'habitat, nous avons sélectionné 13 espèces dont les associations à l'habitat allaient d'une densité de bordure élevée à faible, d'une matrice forestière homogène à hétérogène, d'un étage supérieur de feuillus ou de résineux, de peuplements jeunes ou vieux et de voûte forestière ouverte ou fermée. Nous avons trouvé que les variations dans l'étendue et la configuration du couvert forestier mature ont eu assez peu d'influence sur l'ensemble de la communauté de passereaux de la forêt boréale, mais que les différentes espèces différaient de par leurs réactions à ces variables. Pour être efficaces, les stratégies de conservation de la biodiversité doivent émuler les configurations créées par les perturbations naturelles, en conservant toute la gamme de couverts forestiers homogènes et hétérogènes dans le paysage. Les besoins en matières d'habitat de la moucherolle des aulnes, de la paruline noir et blanc, de la paruline à poitrine baie, de la paruline à gorge orangée, du grimpereau brun, de la paruline masquée, de la paruline à flancs marron, de la moucherolle tchébec, de la paruline couronnée, de la sittelle à poitrine rousse, du viréo aux yeux rouges, du troglodyte mignon et du bruant à gorge blanche correspondent à une vaste gamme de conditions d'habitat qui définissent, de façon minimale, les conditions de filtre brut nécessaires au maintien de la communauté boréale de passereaux en Ontario. Ce groupe d'espèces peut aussi servir à établir un « essai biologique » pour évaluer l'efficacité des politiques forestières de conservation de la biodiversité fondée sur l'imitation des perturbations naturelles.

Dans la partie II du rapport, nous expliquons comment ces scénarios ont été évalués dans le contexte d'une vaste gamme de structures et de configurations de forêt. Cette variété de configurations correspond à ce que les processus naturels de perturbation et de succession devraient produire. Des modèles d'utilisation de l'habitat spatialement explicites ont permis de prévoir les effets de différentes valeurs d'étendue, de composition et de configuration de couvert forestier mature sur l'occupation de l'habitat pour un groupe focal de 13 espèces de passereaux. Nous avons utilisé un programme de planification de la récolte spatialement explicite pour modéliser les options d'aménagement forestier et simuler les conditions futures des forêts qui résulteraient de divers scénarios d'aménagement. Nous avons aussi utilisé un modèle de simulation de feux basé sur les processus pour simuler les conditions futures des forêts qui subiraient de telles perturbations dans des conditions naturelles. Nous avons dérivé la signature des configurations spatiales à la fois pour l'occupation de l'habitat et pour les conditions forestières et nous les avons placées dans le contexte de la gamme simulée de variations naturelles. L'analyse des politiques stratégiques s'est faite dans le contexte des politiques d'aménagement forestier en vigueur en Ontario. Ces politiques concernaient notamment les parcelles séquentielles de récolte limitée dans le temps (créée pour protéger le Caribou des bois) et les zones de récolte différée (créée pour protéger la martre d'Amérique). Cette approche a augmenté le réalisme de l'analyse, mais a réduit la généralité des interprétations.

Dans cette étude, nous avons trouvé que pour être efficaces, les stratégies de conservation de la biodiversité doivent émuler les configurations créées par les perturbations naturelles en maintenant toute la gamme de couverts forestiers homogènes et hétérogènes dans le paysage. On peut réaliser cette variation dans la configuration du paysage en créant des conditions d'habitat favorables à une sélection d'espèces focales qui décrivent collectivement l'ensemble de la niche écologique occupée par la communauté forestière de passereaux. La combinaison des analyses portant sur la communauté et sur les espèces aide à déterminer le groupe d'espèces focales que les aménagistes devraient prendre en considération dans l'élaboration des plans d'aménagement forestier. Fournir un habitat adéquat à tous les membres de ce groupe focal permettra de s'assurer que les besoins importants au niveau « filtre brut » de l'habitat ne sont pas perdus dans le paysage. En définissant les besoins en matière d'habitat pour les différentes espèces du groupe focal, on établit la base d'une stratégie concrète pour déterminer les niveaux et combinaisons appropriés des configurations de paysage nécessaires à la conservation de la biodiversité pour une vaste gamme de passereaux forestiers et peut-être même pour les invertébrés et autres espèces du réseau trophique associés à ces oiseaux. Il faudra mener d'autres études pour évaluer

ces prévisions à différents moments et différents endroits parce que les associations à l'habitat peuvent être influencées par des facteurs déterminants non encore identifiés (p. ex. la distribution de l'abondance des insectes-proies). Bien que plusieurs des associations à l'habitat à l'échelle locale soient assez bien connues, la plupart des associations à l'habitat à l'échelle du paysage sont moins bien comprises. D'autres études seront nécessaires pour évaluer la robustesse des associations à l'habitat aux plus grandes échelles de paysage.

Les résultats de cette étude invitent à adopter des stratégies d'aménagement de la forêt boréale qui créent des zones groupées de haute bordure séparées par de grandes superficies de matrice forestière intacte. C'est la combinaison de ces conditions qui créera la diversité de configurations forestières nécessaire au soutien de toute la gamme de passereaux de la forêt boréale. L'analyse suggère aussi l'emploi de cibles complexes basées sur les simulations de perturbations naturelles. À l'échelle de la communauté, certaines espèces de passereaux sont résilientes dans les bordures, et d'autres le sont moins. C'est seulement en créant la combinaison de conditions que les besoins de filtre brut en matière d'habitat de l'ensemble de la communauté seront comblés. Des modèles quantitatifs d'habitat, spatialement explicites, conçus pour un groupe focal d'espèces de passereaux, décrivent les niveaux et l'ampleur cibles de la variabilité dans les conditions forestières minimalement nécessaires pour permettre la subsistance de toutes les espèces de passereaux de la forêt boréale. L'ampleur simulée de la variabilité naturelle aide à définir la variabilité temporelle à laquelle on devrait s'attendre à la fois pour les variables forestières et les configurations correspondantes d'occupation de l'habitat. L'approche de la modélisation stratégique des configurations à long terme, mais en employant des contraintes opérationnelles réalistes, ajoute validité et complexité à l'interprétation des modèles.

ACKNOWLEDGEMENTS

Julie Elliott (CNFER) provided technical support throughout this project, including management of field studies, data collection, programming and running LSL scripts and editorial assistance on the manuscript. Heather Tumber (Spatial Planning Systems) programmed and ran most of the Patchworks scenario scripts, and Kevin Ride (NRPU) helped refine many of the forest succession pathways. Dave Euler (Birch Point Enterprises), Ian Thompson (Forestry Canada), and Kandyd Szuba (Domtar) provided useful advice and criticisms throughout the project. Steve Gullage (Dalhousie University) and George Holborn (WAP) spent many hours listening and interpreting songbird recordings, and thanks to the many Ontario Summer Employment Program students who collected the songbird recordings in the midst of a forest tent caterpillar outbreak. Thanks also extended to the anonymous reviewers of the original published manuscripts and to Katrina Rempel and Brooke Pilley (CNFER Information Officer) for desktop publishing of the technical report.

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INTRODUCTION

The effect of forest spatial pattern on wildlife habitat, and in particular, the amount, composition, and configuration of young and old forest, is of concern to forest managers because of its potential effect on biodiversity. In the boreal forest, conserving biodiversity requires maintaining habitat for species that prefer mature vs. young forest, hardwood vs. softwood forest, and various levels of mixing and interspersion of these forest types. Creating the right balance is difficult, and is one of the primary reasons that the natural disturbance paradigm has grown in popularity. A principal tenet of the paradigm is that biodiversity can be conserved by harvesting in a manner that resembles forest patterns created by natural disturbance processes (Hunter 1993, Bunnell 1995). Previous research has shown that some songbird species are resilient to changes in age-class and cover-type pattern, but only to a degree (Wedeles and Donnelly 2004, Parker et al. 2005, Schieck and Song 2006). The question of songbird resilience to forest management practices that decrease the amount of mature forest cover and change its configuration should be viewed from the perspective of the overall community response rather than the response of a few individual species. The pressing issue is how to create and assess the complex mixture of forest conditions that is expected to maintain the collective forest songbird community.

The trivial hypothesis that boreal forest songbirds are adapted to conditions of the boreal forest carries with it some interesting conditional assumptions. The boreal forest is dynamic, and its pattern and structure are driven by catastrophic disturbance events such as stand-replacing fire and windthrow (Rowe and Scotter 1973). The more subtle disturbance events—such as death of individual trees or groups of trees caused by insects, disease, and simple senescence—drive within-stand structure. Members of the songbird community should be adapted to a complex landscape pattern replete with edges between young and old forest, and mixtures of stand ages and shade-tolerant vs. shade-intolerant tree species (Hunter 1993, Bunnell 1995, Parker et al. 2005, Schieck and Song 2006). Forest management should consider this full range of natural heterogeneity and homogeneity on the landscape if its objective is in part the conservation of biodiversity. The natural disturbance paradigm suggests that emulating natural disturbance patterns will be sufficient to create this heterogeneity, but practical issues of forest management mean that perfect emulation is never possible. An alternative but complementary approach is to characterize the broad range of habitat conditions associated with the songbird community, and then select a group of focal species that encompasses the broad range of habitat conditions (community niche-space) used by the forest songbird community. Models of the habitat associations for the focal species can then be applied to forest management scenarios. Results of the scenario analyses can be used to assess the relative performance of management options in terms of providing the necessary "coarse-filter" habitat requirements for the songbird community. In this approach, habitat associations of the focal species essentially define the range of variation necessary to sustain the full community.

Linking quantitative habitat models to harvest scheduling models can be used to predict the future consequences of alternative forest management decisions on critical forest pattern and structure variables, and how this translates to predicted habitat occupancy patterns. Likewise, linking habitat and natural disturbance simulation models can be used to evaluate the degree to which projected future habitat conditions deviate from what is expected under a natural disturbance regime. However, a requirement of this approach is that managers must now select the appropriate suite of species for modelling habitat requirements. The natural variability or niche-space model (Figure 1) can help guide the selection of those species.

Complex habitat patterns are not readily characterized by stand-scale resource inventory classifications, whose primary objective is to simplify landscape patterns into homogeneous units for the purpose of accurately estimating merchantable timber volume. Songbirds do not live in the artificial constructs of digitized stand boundaries, and there is no a priori justification to use stand characteristics as the sole means of characterizing a songbird's habitat needs. Stand-scale analyses ignore the influence of adjacent stand conditions and the landscape (matrix) context

in which the stand lies, including the influence of local- and landscape-scale homogeneity and heterogeneity on habitat quality. Habitat selection may be occurring at scales much broader than the traditional stand scale of analysis (Villard et al. 1995, 1999, Wiens 1995, Mitchell et al. 2006) so analysis and modelling methods must reflect this ecological possibility.

MODELLING APPROACH

Some studies have evaluated the effect of spatial harvest constraints on wildlife objectives (Liu et al. 2000, Baskent and Jordan 2002) and others have included non-spatial habitat models in the assessment of projected forests (Rempel and Kaufmann 2003). The model "Seles" (Fall and Fall 2001) has been used to evaluate combined effects of management and natural disturbance on age-class structure (Fall et al. 2004), and other studies have developed and applied spatial habitat models for the evaluation of projected forest conditions (e.g., Arthaud and Rose 1996, Mitchell et al. 2001, Calkin et al. 2002, Johnson et al. 2004, Loehle et al. 2006, Mitchell et al. 2006, Rempel et al. 2006). Only a few studies (e.g., van Damme et al. 2003) have placed spatial habitat evaluations in the context of variability expected under a natural disturbance regime and long-term forest management projections. Rempel et al. (2004) described a process to link proposed management actions to the selection of focal indicator species that are likely to respond to management actions, and Rempel et al. (2006) defined and applied a meta-modelling framework for a management-driven songbird study in Manitoba, Canada, that links various modelling components (including spatial habitat models) for conducting landscape-scale assessments of biodiversity strategies. Our approach to evaluating and assessing biodiversity conservation in a forest management context is described in the following four steps.

1. First we translated the range and dimensions of expected variability in natural disturbance patterns into a complementary model of variability in the dimensions of habitat niche-space (Figure 1).

2. Second we selected an appropriate set of focal species that collectively are adapted to the range of niche-space applicable for the management area.

3. Third we developed spatially explicit habitat models to define the complex arrangement of landscape pattern and habitat elements required by the focal group.

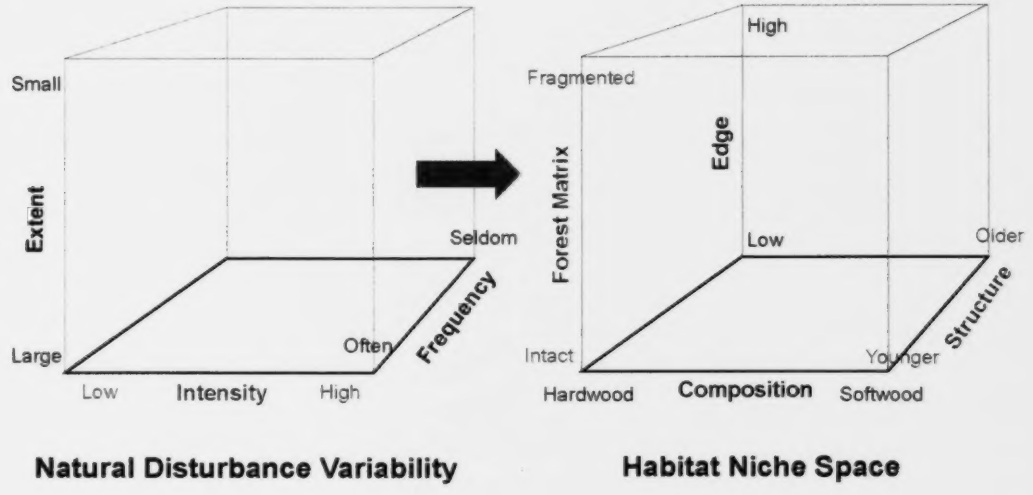


Figure 1. Translation of variability in extent, intensity, and frequency of natural disturbance to habitat niche-space dimensions of patch interspersion, overstory composition, and stand structure.

4. Fourth, we evaluated whether planned management targets support the full range of habitat needs, and whether the arrangement falls within the expected range of natural variation. This approach allows managers to determine more precisely the range of forest characteristics required to sustain the boreal forest songbird community.

This study has been separated into 2 parts:
1) selection of focal songbird species for biodiversity conservation assessment (steps 1-3) and
2) evaluation of alternative forest policy scenarios (step 4).

Part I: Selecting Focal Songbird Species for Biodiversity Conservation Assessment

The steps we used to identify the focal species using spatially explicit sampling and analysis techniques are as follows:

- Establish relationships between forest pattern and composition variables, at local and landscape scales, with relative density for a suite of forest songbirds. As part of this, explore the relative contribution of local- vs. landscape-scale variables in explaining habitat occupancy.
- Develop and test habitat models to quantitatively predict habitat occupancy for individual species.
- Select a suite of focal species based on their relative position within the overall community-niche space, and the relative performance of their predictive habitat models.

Focal, rather than umbrella or other types of indicator species were used because of the value of establishing direct relationships between forest management options and species response (Hannon and McCallum 2004, Rempel et al. 2004), and the ability to define a broad niche-space based on species habitat associations (Figure 1).

Part II: Forest Policy Scenario Analysis

The steps we used to evaluate alternative forest management scenarios, in the context of both policy options and the simulated range of natural variation, are as follows:

- Use the harvest schedule model "Patchworks" (Lockwood and Moore 1993, Baskent and Keles 2005) and associated stand structure and succession curves to project future forest conditions under alternative management strategies that vary the degree of mature forest cover amount and configuration.
- Apply validated spatial habitat models to assess projected future forests.
- Use a newly developed spatial modelling language "LSL" (Kushneriuk and Rempel 2004) to evaluate alternative forest management policy options in terms of sustaining songbird communities.
- Compare and contrast modelling results with expectations under a simulated natural disturbance regime generated by the Boreal Forest Landscape Dynamics Simulator (BFOLDS) (Perera et al. 2004).

PART I: Selecting Focal Species for Biodiversity Conservation Assessment

Methods

Songbird Sampling and Interpolation

Forest songbirds were identified and counted at forest listening stations by using 10-min. recordings of vocalizations made by singing, territorial males, between sunrise and 10:00 am on calm (<25 km/h wind conditions) and rain-free mornings. Bio-acoustic microphones (Hobson et al. 2002, Rempel et al. 2005) were used to record observations in the Rinker Lake (RL) (2002–2004) and Nipigon Forest (NF) (2005) study areas, and for a subset of the Cochrane Study Area (2002–2003) (Rempel et al. 2007).

Alternative point sample designs were simulated and evaluated in terms of their performance for spatial interpolation (Rempel and Kushneriuk 2003) before sampling was initiated. A modified cluster sampling strategy was selected, where sample points were placed in locally dominant habitat types (based on satellite image analysis) in a clustered design. Sample point locations were selected

to provide the spatial dispersion of points that is necessary for spatial interpolation, and to reflect the full range of forested habitat conditions across the study landscape (with the exception of riparian areas).

Songbird sample points were interpolated over a range of just 1 km using ordinary point kriging (Deutsch and Journel 1998) to estimate relative density based on 50 hexagonal analysis cells; thus relative density becomes a function of all points falling within a 50-ha cell, and points adjacent to the cell (Figure 2). Multiple point counts were transformed into a surface, so some important effects of this approach are reductions in the autocorrelation of data records, a reduction in total degrees of freedom for analysis, a decrease in the frequency of observations classed as "absent," and a decreased ability to detect influence of "hard edges" (Figure 2).

Spatial Data Capture

Stand age, height, and standard forest unit (SFU) were captured from the most recent FRI digital maps (1995 photos in NF; 2001 and 2003 photos in CSA), and from these data, percent canopy closure and percent hardwood volume were derived. The FRI maps were first transformed into a raster-like

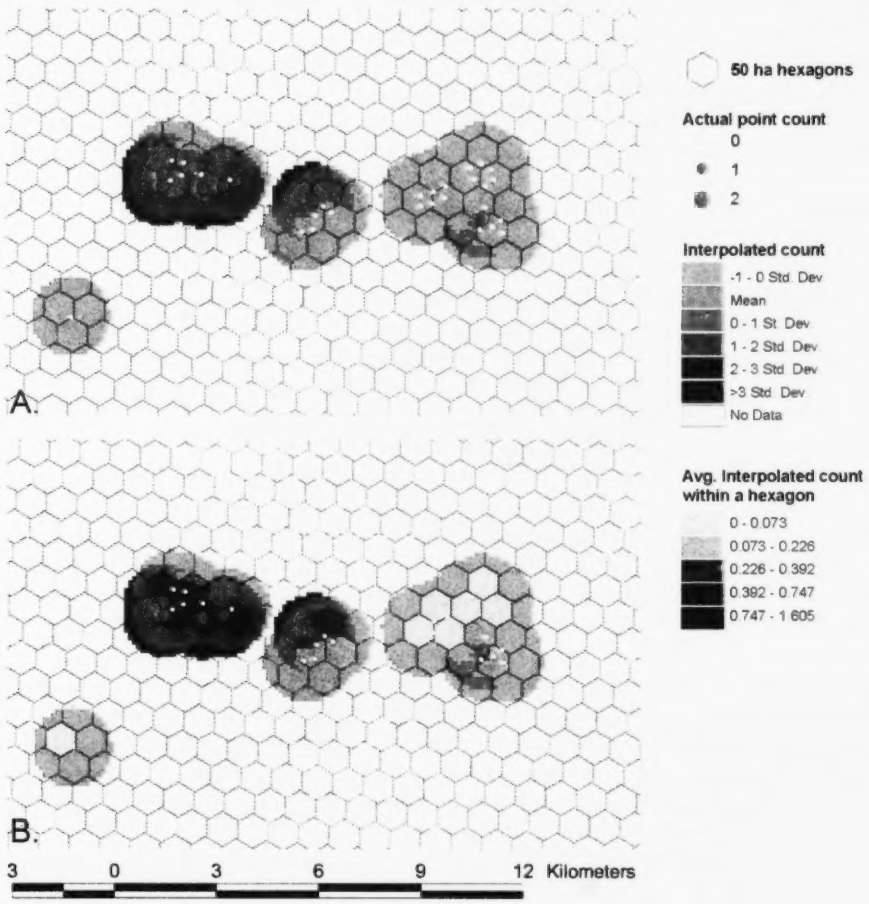


Figure 2. (a) Overlay of 50-ha hexagonal analysis cells on interpolated surface of American Redstart point counts, where interpolation is limited to 1000 m. Only cells that intersect at least one point count are selected for analysis, thus sample size is lower than total number of points; (b) area weighted average of total count is indicated by shade of blue, and estimates the expected total count within a 50 ha hexagon.

grid of 50- and 5000-ha analysis cells using the newly developed Landscape Scripting Language (LSL) created for specialized spatial modelling (Kushneriuk and Rempel 2004). The weighted average of forest age (AGE), tree height (HEIGHT), percent hardwood volume (HARDWOOD), percent canopy closure (CANOPY) and percent young forest (YOUNG) were calculated at the 50-ha scale, and contrast weighted edge-density (EDGE), and percentage of intact mature and old forest matrix (INTACT) were calculated at the 5000-ha scale (Table 1). Edge-density values were then assigned to each of the 50-ha cells falling within the larger 5000-ha cell.

For each of the three explanatory variables, the inter-quartile range (IQR), based on 25th and 75th percentiles, was calculated for the entire study area, and these limits were then used to assign three factor levels (e.g., high, medium, and low) for the two local-scale variables, AGE class and HARDWOOD class, and for the two landscape-scale variables, EDGE class and INTACT class (Table 2).

Table 1. Description of variables (and keywords) used in the habitat models. All variables calculated using hexagonal analysis units generated in LSL.

Variable	Scale †	Acronym	Description
Tree height	Local	HEIGHT	Weighted average of Ontario forest resource inventory (FRI) height, as measured from aerial photography using a parallax bar.
Percent hardwood volume	Local	PHV	A measure of cover-type. Percent of total merchantable timber that is hardwood. Interpolated from yield curves for standard forest units. Low levels indicate softwood cover-type, high levels hardwood cover-type.
Percent canopy closure	Local	PCC	Interpolated from FRI stand age
Average Stand Age	Local	AGE	Weighted average of FRI stand age. Interpretation based on stand height and texture.
Percent Young Forest	Local	PYF	A measure of young forest cover amount. Percent of total forest < 20 years.
Contrast Weighted Edge Density	Landscape	CWED	A measure of forest cover configuration. Contrast weighted density of edge between young (< 20 years old), immature, and mature (> 60) forest, where young/mature forest has a contrast weight of 1, and immature a weight of 0.5
Percent Mature and Old Forest	Landscape	PMOF	A measure of mature forest cover amount. Percent of total forest > 80 years old.

†. Local scale is 50 ha, landscape scale is 5000 ha.

Table 2. Definition of classification variables (factors) used in the ANOVA.

Continuous Variable		Factor level		
	Factor Name	1	3	2
Stand age	AGE-class	<25 years	>70 years	All other
Contrast weighted edge density	EDGE-class	<14 m/ha	>20 m/ha	All other
Percent hardwood volume	HARDWOOD-class	<3 %	>33 %	All other
Percent mature and old forest	INTACT-Class	<25 %	>42 %	All other

Statistical Analyses

Community analysis was performed using Canonical Correspondence Analysis (CCA) (ter Braak and Šmilauer 2002). Its purpose was to estimate components of variance contributed by local- vs. landscape-scale variables, and to visually display species and environmental relationships. Partial CCA analysis was also used to estimate components of variance contributed by local vs. landscape variables, and methods followed those described in Borcard et al. (1992).

Habitat models were created (trained) using binary Bayesian logistic regression (Genkin et al. 2004, 2005) on the balanced sample data set, and the remaining unselected data were used for model testing.

Receiver operating characteristic (ROC) curves (and associated 95% confidence limits) were generated to assess model discrimination accuracy (Pearce and Ferrier 2000) (hereafter, the term ROC statistic refers to the integrated area under the ROC curve). A completely random association of response variable with explanatory variables would result in an ROC approaching 0.5; values above 0.6 indicate a fair fit of the model to the data; values above 0.7 represent a good fit, and values above 0.8 represent a very good to excellent fit (Pearce and Ferrier 2000).

Model reliability was estimated using calibration curves, which relate observed occurrence in the validation field data set to the predicted probability of occurrence from the habitat model (Pearce and Ferrier 2000). Perfect calibration will result in a 1 to 1 relationship where slope = 1 and constant = 0. Bias occurs when the regression constant deviates from 0, and this may occur because of higher or lower prevalence of the species in the validation data set (Pearce and Ferrier 2000). Model spread occurs when the slope deviates from 1, and is of greater concern because it may indicate model misspecification.

Results

Community Response

Partial CCA (Borcard et al. 1992) was used to estimate the independence of local and landscape components of variance at the community level. The variance described by all environmental variables was 0.133, by local variables (after factoring out landscape variables) was 0.095, and by landscape variables (after factoring out local variables) was 0.018. Therefore, only a small component of variance (0.02) was confounded between local and landscape variables. This partial CCA analysis indicates that both local and landscape variables contribute independent information, but that local-scale variables account for about five times more variance than landscape-scale variables (0.095 and 0.018, respectively).

The relationships between environmental variables and species occurrence was described by overlaying the vectors of environmental variables that explain the patterns of co-occurrence (Figure 3). The continuous local-scale variables (HARDWOOD, CANOPY, HEIGHT, AGE, and YOUNG) and landscape-scale variables (EDGE, INTACT) were cast as explanatory variables, and arrows on the CCA biplot depict the direction and strength of the relationship between the explanatory variables and species occurrence.

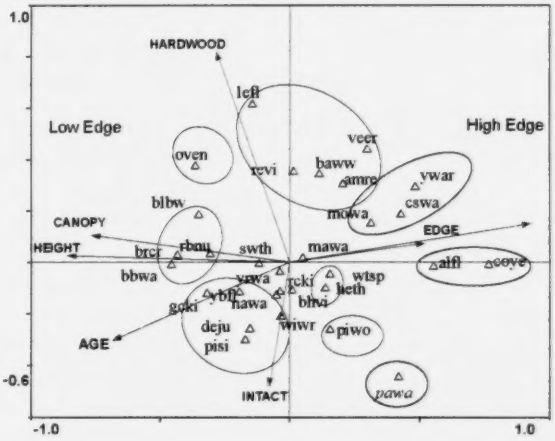


Figure 3. Simple correlations of environmental variables with species occurrence. Arrows show positive correlations only, and points in proximity correspond to species often occurring together. Length of the arrow represents the strength of the association with overall community structure. Species close to the origin show no strong discrimination patterns for the measured environmental variables. Species codes are defined in Table 5.

The CCA reveals four distinct explanatory "factors" associated with species occurrence patterns (p = 0.0020; F = 15.91). The intact forest matrix vector is opposite that of the forest cover type (HARDWOOD) vector, and is separate from that for edge density. The edge density variable, however, is correlated with the local disturbance variable (YOUNG). Finally, the internal stand structure variables CANOPY, HEIGHT, and AGE tend to track together. These responses can be interpreted as four separate factors: (1) overstory composition (HARDWOOD), (2) forest cover configuration (EDGE), (3) intactness of the forest matrix (INTACT), and (4) development of stand internal structure (AGE/CANOPY/HEIGHT).

The ordination analysis supports the notion that the landscape-scale variable, INTACT, contributes explanatory information that is independent from local-scale variables. INTACT is a measure of intactness of the mature forest matrix, and is only weakly correlated with the local-scale variable AGE. However, EDGE is highly correlated with the local-scale variable YOUNG. YOUNG is a measure of the relative amount of young forest at the 50-ha scale, whereas EDGE is a measure of the configuration of young and old forest at the 5000-ha scale.

The ordination indicates that individual species within the boreal songbird community are associated with a range of cover type, stand age, disturbance intensity, and forest matrix conditions. Individual species have specific environmental needs, but the overall community requires a broad range of environmental conditions. Overlaying isopleths that model the relationships between individual environmental variables helps give concrete meaning to the rather abstract ordination. Isopleths of equal edge density are illustrated in Figure 4, and reveal that Veery (*Catharus fuscescens*), Yellow Warbler (*Dendroica petechia*), Alder Flycatcher (*Empidonax alnorum*), and Common Yellowthroat (*Geothlypis trichas*) are all associated with high edge density (>20 m/ha), whereas Bay-breasted Warbler (*Dendroica castanea*), Brown Creeper (*Certhia americana*), Ovenbird (*Seiurus aurocapilla*), and Red-breasted Nuthatch (*Sitta canadensis*) are associated with low edge density (<18.5 m/ha) (Figure 4). Those species responding significantly to the edge variable are highlighted in bold in the figure.

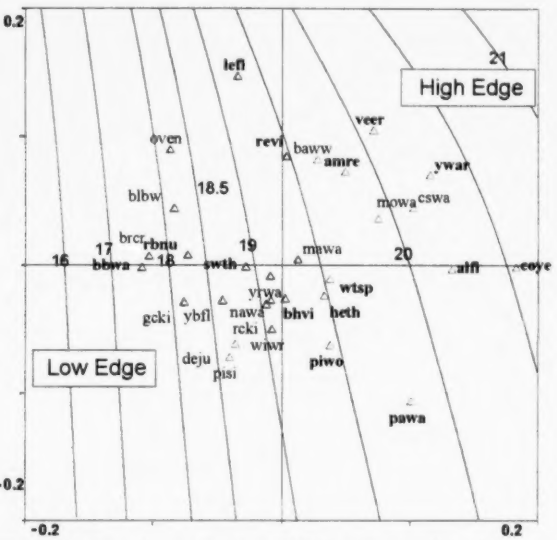


Figure 4. Species ordination (CCA), with overlay of isopleths (GLM) for contrast weighted edge density (EDGE) in m/ ha. Isopleths delineate species predicted to occur in areas of low to high density of edge.

Likewise, there are patterns of discrimination for intact forest at the landscape scale. Species such as Red-eyed Vireo (*Vireo olivaceus*), Veery, and Chestnut-sided Warbler (*Dendroica pennsylvanica*) are associated with low levels of intact mature forest cover (<32%), whereas Dark-eyed Junco (*Junco hyemalis*), Pine Siskin (*Carduelis pinus*), Pileated Woodpecker (*Dryocopus pileatus*), and Winter Wren (*Troglodytes troglodytes*) are associated with a forest matrix with higher levels of intact mature and old forest (Figure 5). At the local scale, patterns of discrimination are evident for both cover type and average stand age. Note that the ordination pattern for HARDWOOD (Figure 6) vs. AGE (Figure 7) is almost orthogonal; hardwood conditions are important for both young and old stands, and do not simply represent an early successional condition.

When conditional (partial correlation) environmental vectors are overlaid (Figure 8), five relatively strong and orthogonal groupings of explanatory variables (factors) emerge: HARDWOOD, HEIGHT, CANOPY, INTACT/AGE, and YOUNG/EDGE. A consequence of modelling partial correlation is that the importance of forest configuration (EDGE) becomes much smaller relative to the amount of young forest (YOUNG).

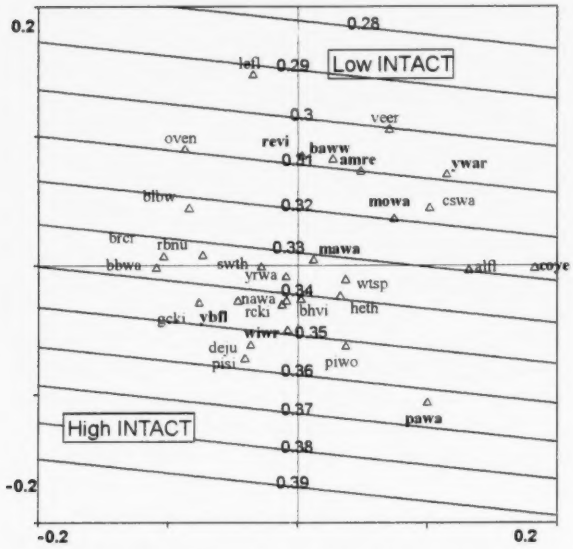


Figure 5. Species ordination (CCA), with overlay of isopleths (GLM) for proportion mature and old forest (INTACT). Isopleths delineate species predicted to occur in areas of low to high proportions of intact mature forest.

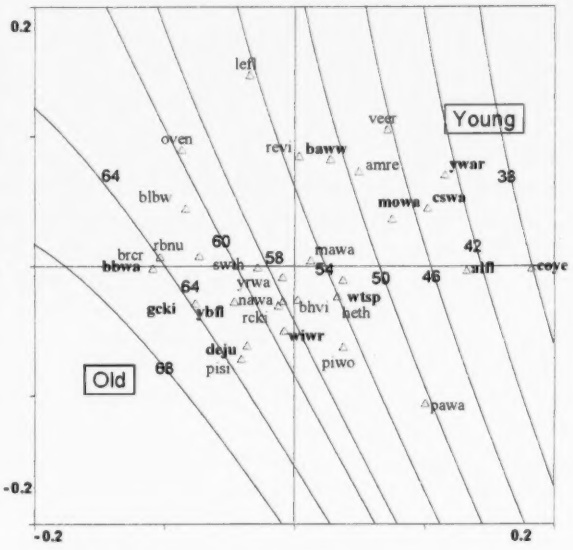


Figure 7. Species ordination (CCA), with overlay of isopleths (GLM) for stand age (AGE) in years. Isopleths delineate species predicted to occur in areas of young to old forest.

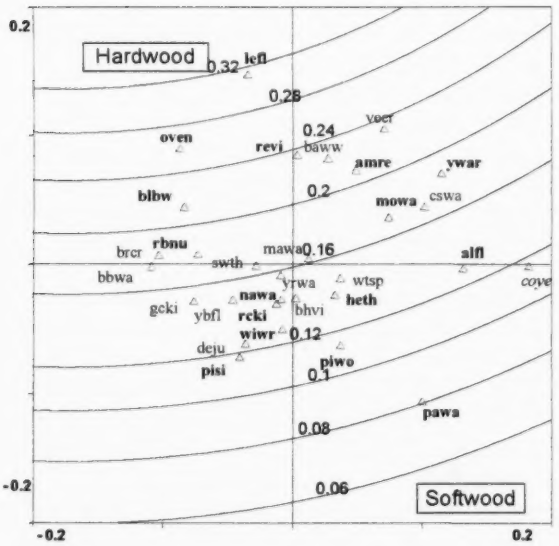


Figure 6. Species ordination (CCA), with overlay of isopleths (GLM) for percent hardwood volume (HARDWOOD). Isopleths delineate species predicted to occur in areas of low to high proportions of hardwood forest.

Interpretation of the ordination figure reveals at least ten natural groupings of species that collectively define a broad range of environmental conditions on the landscape:

1. Older, tall, closed canopy hardwood, with little interspersion of young and old forest: Ovenbird.
2. Immature to younger hardwood, with relatively open conditions: Least Flycatcher (*Empidonax minimus*), Red-eyed Vireo, Black-and-white Warbler (*Mniotilta varia*), American Redstart (*Setophaga ruticilla*), and Veery.
3. Younger hardwood, open canopy, interspersion of young and old forest: Yellow Warbler, Chestnut-sided Warbler, Mourning Warbler (*Oporornis philadelphia*).
4. Young mixedwood, open canopy, interspersion of young and old forest: Alder Flycatcher, Common Yellowthroat.
5. Old, open, conifer bogs: Palm Warbler (*Dendroica palmarum*).
6. Older, open, softwood stands in a mature forest matrix: Pileated Woodpecker.
7. Older, closed, softwood forest, in a mature forest matrix: Winter Wren, Dark-eyed Junco, Pine Siskin, Yellow-bellied Flycatcher (*Empidonax flaviventris*), Golden-crowned Kinglet.
8. Older, closed, mixedwood (hardwood and softwood dominated types), with little

interspersion of young and old forest: Bay-breasted Warbler, Brown Creeper, Red-breasted Nuthatch, Blackburnian Warbler (*Dendroica fusca*).

9. Open mixedwood, high edge density: White-throated Sparrow, Hermit Thrush (*Catharus guttatus*).
10. Species without strong patterns of discrimination for the measured variables: Magnolia Warbler (*Dendroica magnolia*), Swainson's Thrush (*Catharus ustulatus*), Yellow-rumped Warbler (*Dendroica coronata*), Blue-headed Vireo (*Vireo solitarius*), Nashville Warbler (*Vermivora ruficapilla*), Ruby-crowned Kinglet (*Regulus calendula*).

This grouping of species provides critical information for making an informed and unbiased selection of focal species for modelling and monitoring environmental effects of forest management. If species are selected from only one quadrant of the ordination figure, then management assessment would be biased toward a restricted set of environmental conditions and species response.

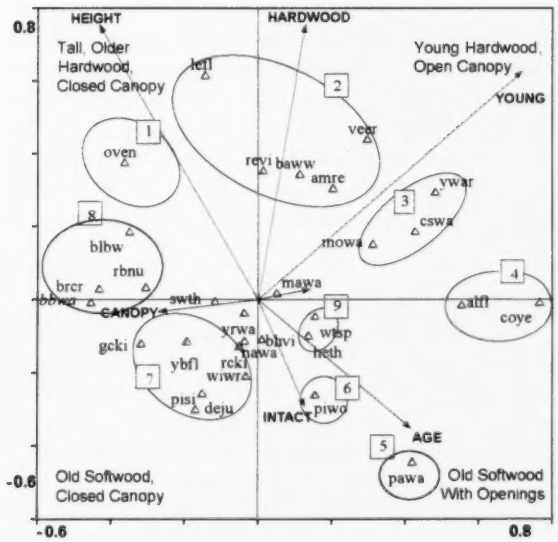


Figure 8. Partial correlations (conditional effects) of standardized environmental variables with species occurrence, where conditional effects are represented by arrows pointing in the direction of positive associations, assuming the other environmental variables are held at their mean values. Length of the arrow represents the component of variance accounted for by that factor in predicting overall community structure.

Habitat Model Performance and Focal Species Selection

Canonical correspondence analysis ordination figures do not easily translate into testable management objectives, so RSPF habitat models were developed to predict the probability of habitat occupancy based on local-and landscape-scale variables. The habitat models essentially translate forest cover amount and configuration into probabilities of habitat occupancy, and consequently are of great value for evaluating alternative forest management options (and resulting forest configurations) for biodiversity conservation. In general, the logistic regression model coefficients reflect the direction of partial correlations (Figure 8), but there were a few exceptions. For example, CCA analysis suggested Yellow-bellied Flycatcher would be associated with older forest with greater canopy closure, but the logistic regression resulted in an opposite association.

Model discrimination was tested using ROC values, and for training data these ranged from 0.6 to 0.85. The ROC values were also calculated for model test (validation) data to evaluate consistency of model discrimination. Models with the highest ROC values (i.e., >0.8) almost always had test ROC values lower than the 95% confidence limit. This suggests that model discrimination was inconsistent for these species.

Model reliability was tested using calibration curves, and model spread ranged from 0.47 to 1.12. Models where the slope approaches unity (i.e., the 95% C.L. for the slope brackets 1) indicate the model is reliable in terms of systematically predicting relative species occurrence. Models with low reliability (e.g., American Redstart, Golden-crowned Kinglet, Nashville Warbler, and Pileated Woodpecker) also had inconsistent discrimination, where ROC test values fell well below the 95% C.L.. Model bias was estimated by the model constants, and 11 of 30 models had constants where the 95% C.L. did not encompass 0, indicating some level of bias. This probably occurs because the species is either more prevalent or less prevalent in the test data relative to the

training data. This can lead to a consistent over or underestimation of the probability of occurrence. Model spread, however, is of greater concern because it indicates model misspecification.
The selection of focal species is based on a combination of study objectives and evaluation of species' model performance. Overall model performance was considered high when: (1) CCA analysis agreed with logistic regression analysis, (2) model discrimination among observations was >0.7, (3) model discrimination was consistent among training and testing sites, and (4) model predictive reliability was high, with model spread (i.e., slope) approaching unity. Where the objective is to select species that represent a broad range of forest diversity (niche-space) as revealed through the CCA analysis, then Hermit Thrush, Veery, Brown Creeper, Pine Siskin, Alder Flycatcher, Ovenbird, and Palm Warbler all represent this diversity and have models that perform well in terms of consistency, discrimination, and reliability.

In contrast, study objectives may be focused on more specific forest attributes, such as forest cover amount and configuration at the landscape scale. In such cases, evidence of a significant response to those attributes becomes a dominant factor in the selection of focal species. This imposes restrictions on model selection, and can lead to compromises on setting acceptable model performance.
The selection of focal species suggested for assessing (in part) the sustainability of proposed forest management policy options was based on a species' position within the environmental ordination (Figure 3) and the assessment of model performance. Thirteen species were selected as focal species for this second objective, and their RSPF model coefficients (Table 3) define a broad array of habitat conditions that reflect the diversity of forest conditions expected at the landscape scale. This selection of focal species, however, includes a few models that performed relatively poorly. Those models were selected only because the species revealed a significant (p <0.05) response to either forest cover configuration or amount of intact forest at the landscape scale, and there was no other alternative species with a better performing model. To reflect the variability of confidence in habitat models, the influence of the model in assessing policy options can be weighted by the model discrimination test score (Rempel et al. 2007).

Discussion

In this study, we ignored stand boundaries, and instead characterized habitat at local (50 ha), and landscape (5000 ha) scales, and found that for 19 of 30 species the area of influence on songbird habitat use extended up to 5000 ha. Forest configuration, i.e., the edge between young and old forest, and the homogeneity of the intact

Table 3. Model coefficients and constant (C) for logistic regressions of habitat occupancy.

Species	AGE	AGE²	HEIGHT	HEIGHT²	PYF	PCC	PCC²	PHV	PHV²	CWED	CWED²	PMOF	C†
Alder Flycatcher	0.020	0.000	0.236	-0.014	-0.132	-0.173	0.002	0.464	0.169	0.131	-0.003	1.331	0.594
Black-and-white Warbler	0.006	0.000	-0.096	-0.001	0.000			0.827	0.218	-0.011		-3.596	0.584
Bay-breasted Warbler	-0.002	0.000	0.314	-0.017	-3.111	-0.066	0.000	0.000	-0.707	-0.262	0.006	1.512	3.189
Blackburnian Warbler		0.000	0.070	0.000	-1.052		0.000	0.564				1.110	-1.631
Brown Creeper	0.003	0.000	0.265	0.002	0.450	-0.001	0.000	-4.358	5.306	0.046	-0.002	1.418	-3.578
Common Yellowthroat	0.056	0.000	-0.706	0.022	0.862	-0.087	0.001	4.880	-6.184	0.552	-0.013	-0.543	-3.352
Chestnut-sided Warbler	0.050	0.000	0.507	-0.009	0.928	-0.156	0.000	-1.461	3.874	0.022	-0.001	0.387	-2.383
Least Flycatcher	-0.002			0.003		-0.020		2.118	-0.643	-0.021		-1.388	0.066
Ovenbird	-0.012		0.134	-0.002	-2.258	-0.051	0.000	9.001	-9.145	-0.186	0.003	-0.657	4.340
Red-breasted Nuthatch	0.019	0.000	0.189	-0.004	0.000	0.020	0.000	2.401	-3.530		-0.001	1.866	-2.138
Red-eyed Vireo		0.000	-0.686	0.032	-3.141	-0.088	0.001	9.011	-8.072	0.159	-0.003	-2.085	5.855
Winter Wren	0.027	0.000	-0.073	-0.006	-1.964	-0.023		-2.330	3.131	0.081	-0.001	5.494	0.487
White-throated Sparrow			-0.086					1.262	-2.589		0.001	4.642	1.343

†. Constant

forest matrix had significant effects on habitat use. Partial CCA analysis revealed that both local and landscape-scale variables contributed independently to explained variance. At the local scale, the stand-structure effects of average stand age and percent hardwood volume had strong and predictable effects, but for 19 species, significant additional components of variance in songbird relative abundance were accounted for by including landscape-scale variables. The value of a local site as habitat to a bird is influenced by the composition and homogeneity (or heterogeneity) of the surrounding landscape. This has implications for forest management, in that broad landscape-scale patterns of forest disturbance may indeed influence habitat use by songbirds. Development of biodiversity conservation strategies must consider landscape-scale patterns such as the relative area of mature forest cover, and the configuration of cover in terms of forest edge.

Modeled gradients of habitat association for the 13 species selected as focal species for evaluation of forest policy options (Alder Flycatcher, Black-and-white Warbler, Bay-breasted Warbler, Blackburnian Warbler, Brown Creeper, Common Yellowthroat, Chestnut-sided Warbler, Least Flycatcher, Ovenbird, Red-breasted Nuthatch, Red-eyed Vireo, Winter Wren, and White-throated Sparrow), all generally agree with previously published findings. For example, on relatively moderate forest-cover gradients we found Alder Flycatcher, American Redstart, Black-and-white Warbler, Common Yellowthroat, Chestnut-sided Warbler, Least Flycatcher, Mourning Warbler, Red-eyed Vireo, Veery, and White-throated Sparrow are associated with higher disturbance intensities, with less intact mature forest cover, and higher levels of age-class interspersion. Webb et al. (1977) studied a gradient of disturbance intensity (0, 25, 50, and 75% harvest removal) over 7 years in the Adirondacks and, even though the ecoregion is markedly different, also found American Redstart, Chestnut-side Warbler, Black-and-white Warbler, and Veery all tended to increase with harvest intensity. Similarly, in Ontario, Freedman et al. (1981) found Chestnut-sided Warbler, Common Yellow-throat, and White-throated Sparrow to be associated with younger forest, and Welsh (1987) found White-throated Sparrow, Chestnut-sided Warbler, Mourning Warbler, and Alder Flycatcher to be associated with early successional habitat.

In contrast, we found that Bay-breasted Warbler, Blackburnian Warbler, Brown Creeper, Golden-crowned Kinglet, Ovenbird, Red-breasted Nuthatch, and Winter Wren are associated with conditions of lower disturbance intensities, including greater levels of intact mature forest cover and less age-class interspersion. Webb et al. (1977) also found Blackburnian Warbler, Least Flycatcher, Ovenbird, and Winter Wren tended to decrease with harvest intensity, and for all but Least Flycatcher, agreed with results here. Likewise, Welsh (1987) found Bay-breasted Warbler, Golden-crowned Kinglet and Ovenbird to be associated with late-successional habitat. The results for Least Flycatcher disagreed with those of Webb et al. (1977); however Holmes and Sherry (2001) found Least Flycatcher to be strongly associated with early successional habitat.

Habitat fragmentation generally refers to two factors, the loss of habitat and the breaking apart (configuration) of habitat, and consequently requires at least two separate measures to quantify area-sensitive vs. edge-sensitive responses (Fahrig 1997, Schmiegelow and Monkkonen 2002). Although INTACT-class was used to measure amount of mature forest cover, and EDGE-class to measure configuration of forest cover, the study design did not allow complete separation of these factors. For example, a decline in INTACT will generally result in some increase in age-class edge (EDGE) because the area of forested land does not change temporally or spatially. Regardless of the partial dependencies, the data were only weakly collinear, and the ordination revealed almost orthogonal responses, with species like Bay-breasted Warbler and Red-breasted Nuthatch responding negatively to the configuration of mature forest (EDGE), and Winter Wren responding negatively to forest cover loss (INTACT). There was also considerable overlap in the ordination, with many species responding to both EDGE and INTACT. For the ordination and regression, YOUNG, a measure of the relative abundance of young forest at the local scale, was used to characterize loss of mature forest (or gain in young forest). Logistic regression analysis was used to assign relative weights of the model variables for predicting habitat occupancy, and in general, the results are similar to those found by Trzcinski et al. (1999) in that relative amount of mature forest cover was a stronger predictor of

habitat occupancy than the configuration of forest cover.

A factorial, randomized block design was used to compartmentalize the components of variance resulting from local- vs. landscape-scale variables. This approach helps strengthen the conclusion that landscape-scale effects were important; however, they leave unaddressed whether 5000 ha is the most appropriate scale for assessing forest edge and matrix conditions. The CCA analysis suggested strong correlation between the landscape-scale variable EDGE, and the local-scale variable YOUNG. The terms local and landscape have no intrinsic meaning, and 50 ha may be considered by some to be a landscape-scale variable. Regardless, both these variables will increase with greater disturbance intensity. Future studies should explore this relationship by characterizing the two variables over a greater division of scales. In contrast, the landscape-variable INTACT did not have any strong correlation with local-scale variables.

The CCA ordinations help visualize patterns of association. For example, Figure 4 identifies which species are associated with high vs. low edge (in m/ha) by identifying the general associated levels of edge density, and Figure 5 does likewise for the intactness of the forest matrix. From a songbird community perspective, species are associated with a broad range of landscape patterns, ranging from high to low edge and intactness of the forest matrix, and at the local scale, high to low levels of forest disturbance, canopy closure, and early successional tree species.

The songbird community requires disturbance to provide the range of habitat conditions to which the species are adapted. For example, some species such as Bay-breasted Warbler and Red-breasted Nuthatch are associated with conditions found in low levels of disturbance, including low levels of edge, low levels of hardwood, older forest, and closed canopy. Other species such as Common Yellowthroat, Alder Flycatcher, and Yellow Warbler are associated with higher levels of disturbance, and these species apparently require disturbance for the creation of quality habitat.

PART II: Forest Policy Scenario Analysis

Methods

Meta-model

The scenario analysis framework can be viewed as a linked set of models that includes habitat, wood supply, yield curve, harvest scheduling, spatial landscape assessment, stand structure, stand succession, and natural disturbance modelling components. We termed the overall framework a spatial landscape assessment meta-model (Figure 9). The meta-model visually depicts links between data and modelling components described below.

Habitat Models

We used spatially explicit, multiple-scale habitat models to predict the relationship between local-scale (50 ha) and landscape-scale (5000 ha) forest variables and the probability of habitat occupancy for a focal set of 13 forest songbird species. Models were developed and tested in a related study using three locations in the northern boreal region of Ontario (Rempel 2007). Rinker Lake (RL), on the west side of Lake Nipigon, and the Nipigon Forest (NF) on the east side of Lake Nipigon are in dry-humid boreal conditions, and the Cochrane Study Area (CSA), which includes the northern part of the Claybelt region, is located

Spatial Landscape Assessment Meta-Model

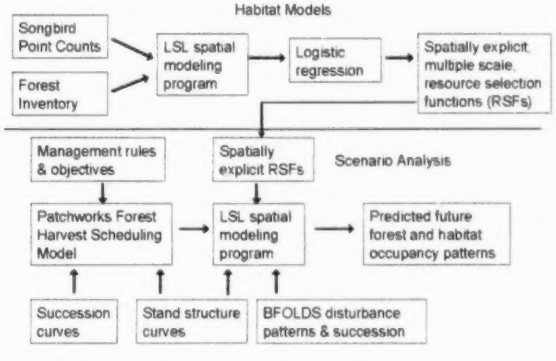


Figure 9. Schematic diagram (meta-model) of links between model components, flow of data, and model outputs. Upper figure describes habitat modeling components, and lower figure describes scenario analysis components.

in medium-humid boreal conditions (Figure 10). All areas are located in forest management units with active logging. In scenario analysis figures, the term "high probability of habitat occupancy" refers to sites with probabilities of habitat occupancy above a critical threshold for correctly assigning the occupied or unoccupied label. All habitat models had a discrimination index (ROC value) >0.65, indicating a fair-to-good ability to, on average, assign higher probability of habitat occupancy to occupied sites and vice versa (Figure 11). Species selected for scenario analysis represent a broad array of habitat associations, or niche-space (Figure 1), and include species that are apparently resilient and non-resilient to landscape-scale patterns of contrast weighted edge-density (EDGE) and percent intact mature and old forest (INTACT). To meet the scenario analysis objectives of this study, it was critical to select species that occupied as many "corners of the box" (Figure 1) as possible. Although the preferred minimum level of model discrimination was 0.70 for selecting the focal species, the niche-space requirements were critical, and this resulted in the selection of some species models with only fair discrimination and calibration levels (Rempel 2007).

Spatial Forest Projection

Alternative forest management scenarios were simulated using Patchworks, a harvest scheduling program that generates forest harvest solutions in the context of vegetation succession, stand development, and forest management constraints (Lockwood and Moore 1993, Baskent and Keles 2005). Three management scenarios were simulated:

1. Forest management under non-spatial guidelines (NOSPATIAL) only, such as silvicultural guidance for replanting, tending, and harvest volume objectives.

2. Silvicultural guidelines plus all featured value guidelines (ALLGUIDES) as specified in Ontario's natural pattern emulation (NPE), timber management guidelines for marten (*Martes americana atrata*), moose (*Alces alces*), caribou (*Rangifer tarandus*), and fish habitat (Ontario Ministry of Natural Resources (OMNR) 1988a, 1988b, 1996, 2002, Racey et al. 1999).

3. Silvicultural guides plus natural composition targets (NATURAL) based on previous natural disturbance BFOLDS simulations (Table 4).

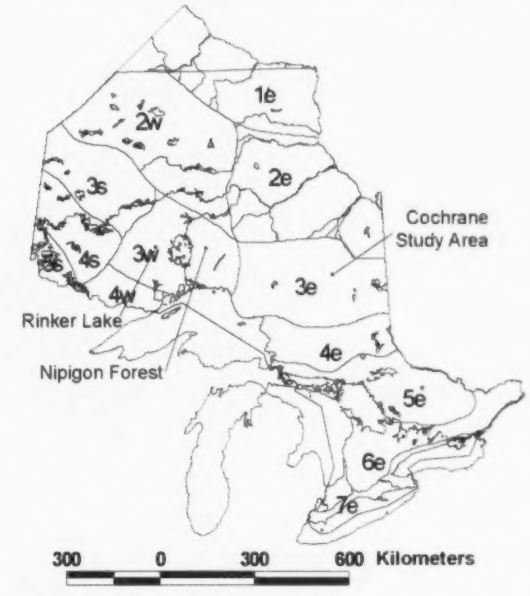


Figure 10. Location of Rinker Lake, Nipigon Forest, and Cochrane Study Area study sites. Ecoregions based on Hills (1961), where 5S, 4S, and 3S are sub-humid, 4W and 3W are dry-humid, and 3E and 2E are medium-humid.

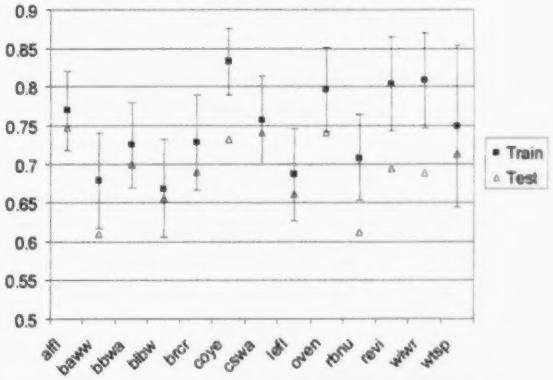


Figure 11. Accuracy assessment (ROC) and 95% confidence limits for the focal species habitat models. Values are area under the ROC curve, and represent the probability of correctly assigning the correct label (occupied/unoccupied) for new observations. Closed symbols are for model development (training), and open symbols for independent testing of the models.

Table 4. Description of the four conditions (current forest and three management scenarios) used in the scenario analysis.

Scenario	Keyword	Description
Current State of the Forest (year 2001)	CURRENT	Current state of the forest based on latest FRI.
No Spatial Guidelines	NOSPATIAL	Basic silvicultural policies and practices are simulated along with a realistic transportation budget and operational rules (e.g., winter harvest areas), but no spatial harvest pattern objectives are defined. Harvest volume targets based on existing supply commitments.
All Featured Values Guidelines	ALLGUIDES	NOSPATIAL silvicultural parameters, plus spatial pattern objectives based on guides for featured species (marten and caribou), the fish habitat guides, and non-spatial old-growth targets and harvest pattern from NDPEG. Harvest volume targets based on existing supply commitments.
Natural Composition Targets	NATURAL	Landscape Mosaic Scenario. Compositional targets set to emulate natural disturbance patterns and composition. The first set of objectives was derived from an analysis of BFOLDS runs for the entire ecoregion 3W. Minimum amounts of mature forest pattern class were used in a quasi-spatial SFMM. The strategic solution for the ecoregion was to harvest the Lake Nipigon Forest more aggressively than the current AHA (while reducing harvest levels on other FMUs below current AHAs). We used the resulting composition of the SFMM solution on Lake Nipigon as the objectives. Harvest volume targets were allowed to fluctuate through time.

The current state of the forest (CURRENT) represents a mix of natural disturbance events, gap dynamics, and timber management guidelines that have been applied over the last 60 or so years in the NF Management Unit. Only the ALLGUIDES scenario had spatial and temporal constraints to logging (caribou blocks, marten cores, and NPE old-growth and spatial targets), and these affect broad patterns of harvest eligibility (Figure 12). Based on initial exploratory analysis of scenarios, NOSPATIAL, ALLGUIDES, and NATURAL scenarios were all set to achieve 100% of harvest using harvest patches of 100–1000 ha (where a patch is a clump of touching harvest blocks) to reduce unrealistically high levels of age-class fragmentation across the landscape.

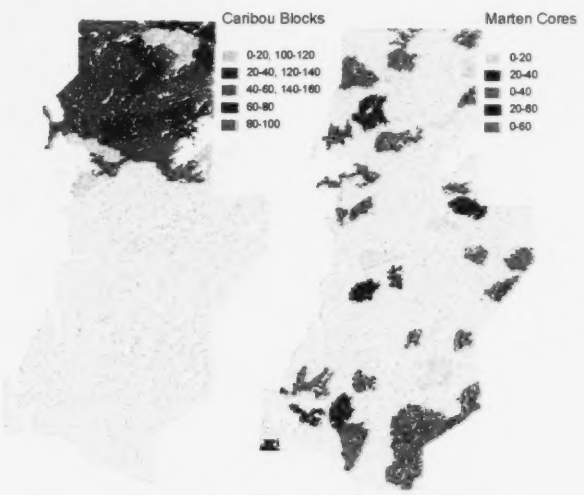


Figure 12. Sequential timings (years from present) for when blocks are available for harvest (Caribou Blocks), and for when reserve blocks are unavailable for harvest (Marten Core Areas) in the Lake Nipigon forest management unit. These timings are used in both the existing spatial harvest guidelines.

Habitat element curves were developed to project changes in tree height and percent canopy closure over time (Figure 13), and were based on analysis of Ontario growth and yield data (Elkie et al. 2004). Curves were created by fitting second-order polynomial equations to the data, and each plot was reviewed and in some cases revised using expert opinion to create the final plots and look-up tables. Separate look-up tables were created

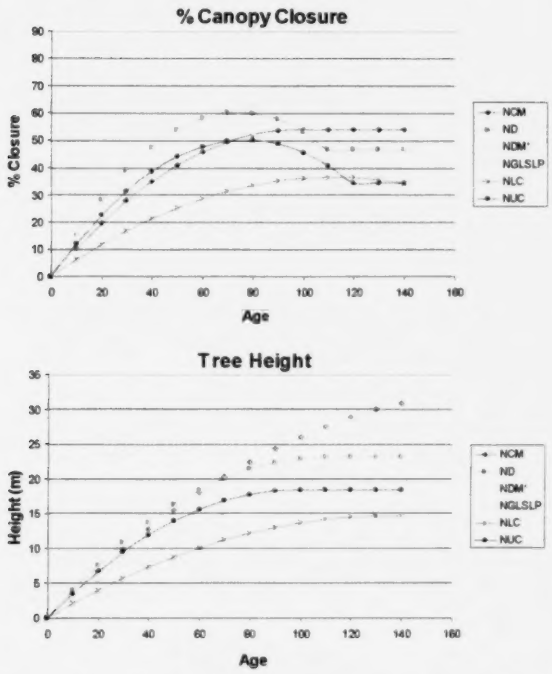


Figure 13. Habitat element curves (HECs) for percent canopy closure and tree height (m) for northern upland conifer (NUC), northern lowland conifer (NLC), northern conifer mixed (NCM), northern deciduous (ND), and northern deciduous mixed (NDM). *Data for north deciduous mixedwood (NDM) were not available and we have used south deciduous mixedwood as an estimate.

for upland conifer, lowland conifer, deciduous, deciduous mixedwood, Great Lakes–St. Lawrence pines, and conifer mixedwood.

Spatial Pattern Analysis and Simulated Range of Natural Variation

Spatial environmental and species response data were captured using the recently developed spatial analysis programming language, LSL (Kushneriuk and Rempel 2004). A hexagonal grid of 7-ha cells was used to build a nested set of pseudo-hexagons, or gridsets, of increasingly larger size. A 5000-ha gridset was selected for the broadest scale of analysis (landscape scale), and 50 ha for the local scale. At 5000 ha, the linear distance from the center of the hexagon to the edge is between 3.5 and 4 km, corresponding to the approximate range (linear distance) of spatial auto-correlation among songbird point counts (approx. 5 km) (Rempel 2007). The 50-ha scale corresponds to the approximate area surveyed by a cluster of songbird point listening stations (maximum 150 m listening range).

Natural disturbance, and the associated range of variation, was simulated using BFOLDS (Perera et al. 2004), which is a process-based model, where model components such as ignition and fire-spread rates are based on previously published research findings. The model creates simulated maps of future forest conditions expected under a natural disturbance regime. For each map, a histogram of the simulated variable was created (Figure 14). The simulation was repeated 72 times (three burn intensities and eight replications for simulation years 100, 150, and 200) to generate 25th and 75th percentiles for each histogram bar. This simulated range of natural variation (SRNV) is denoted on the histograms by upper and lower "*". The RSPF models were also applied to BFOLDS simulations to create SRNV values for habitat occupancy classes.

Results

Habitat Model Characteristics

The spatial habitat models for the 13 focal species were applied to the current forest resource inventory (FRI) maps, and mean values for model forest variables were summarized for areas of high probability of habitat occupancy vs. low probability (Table 5). These emergent averages summarize the typical forest conditions that the habitat models predict would be associated with the best habitat. For example, the model predicts that Alder Flycatcher (*Empidonax alnorum*) will be associated with a 13.9% decrease in CANOPY, a 4.1 m decrease in average HEIGHT, a 17% increase in HARDWOOD, and a 9.9 m/ha increase in EDGE. Overall, the 13 models characterize a broad range of habitat conditions at the local and landscape scale that would likely be associated with a natural and diverse forest region. The models can be grouped into five rough categories:

1. *Younger, more open hardwood forest, with high disturbance and edge levels:* Alder Flycatcher, Black-and-white Warbler (*Mniotilta varia*), Chestnut-sided Warbler (*Dendroica pennsylvanica*), Common Yellowthroat (*Geothlypis trichas*).

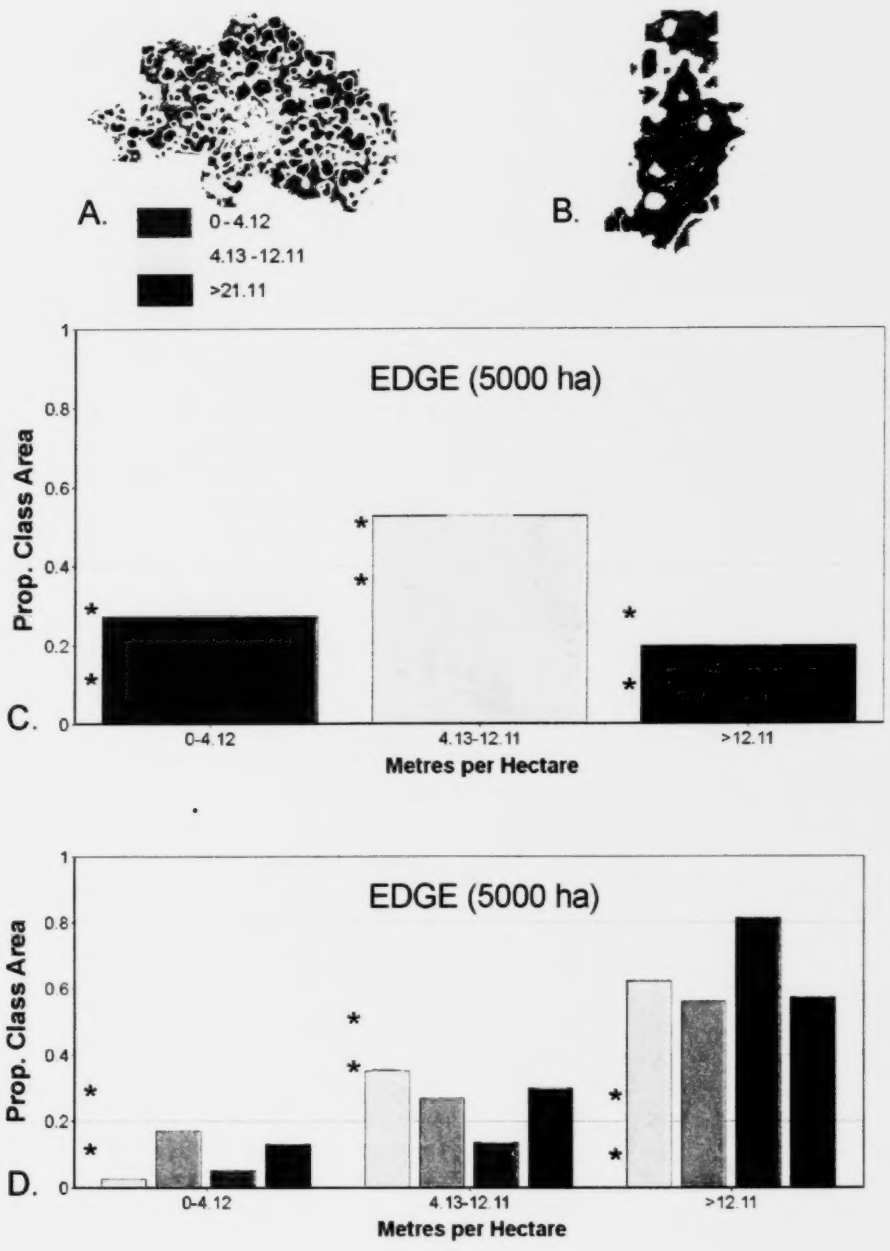


Figure 14. Development and application of simulated range of natural variation (SRNV), and spatial pattern signatures: (A) 1 of 72 natural disturbance simulation maps (using BFOLDS) for ecoregion 3W, (B) projected map of EDGE (using Patchworks) for Nipigon Forest under the no spatial guides (NOSPATIAL) management scenario, (C) proportion of map-area with low, medium, and high contrast weighted edge density (EDGE), where asterisks are 25th and 75th percentiles for histogram heights among all 72 replications for ecoregion 3W, (D) proportion of Nipigon Forest map-area with low, medium, and high EDGE, among four scenarios, and where asterisks represent SRNV for EDGE from (C) above.

2. *Older softwood mixedwood, lower edge, higher intact forest:* Bay-breasted Warbler (*Dendroica castanea*), Blackburnian Warbler (*Dendroica fusca*), Brown Creeper (*Certhia americana*), Red-breasted Nuthatch (*Sitta canadensis*), Winter Wren (*Troglodytes troglodytes*).

3. *Older, open mixedwood, more intact forest:* White-throated Sparrow (*Zonotrichia albicollis*).

4. *Closed hardwood, more disturbance, less intact forest:* Red-eyed Vireo (*Vireo olivaceous*), Least Flycatcher (*Empidonax minimus*).

5. *Closed hardwood, less disturbance and edge, less intact forest:* Ovenbird (*Seiurus aurocapillus*).

In general, the models agree with common field observations and understanding of habitat associations, especially at the local scale (Rempel 2007). One exception may be the Least Flycatcher, where some studies suggest this is more of a forest interior species. Nonetheless, this species was associated with younger (but closed) hardwoods in all three study areas.

Table 5. Difference in habitat variable averages for high vs. low probability of habitat occupancy, when the habitat models are applied to the current forest inventory.

Common name	AOU code	Latin name	CANOPY	HEIGHT	Local			Landscape	
					YOUNG	AGE	HWD	EDGE	INTACT
Alder Flycatcher†	ALFL	*Empidonax alnorum*	-13.9	-4.1	0.24	-10.1	-0.17	9.9	-0.01
Black-and-white Warbler	BAWW	*Mniotilta varia*	-2.4	-3.2	0.04	-31.7	0.14	1.2	-0.52
Bay-breasted Warbler	BBWA	*Dendroica castanea*	0.2	0.2	-0.16	15.5	-0.16	-5.1	0.17
Blackburnian Warbler	BLBW	*Dendroica fusca*	8.1	4.6	-0.17	34.6	0.01	-4.9	0.47
Brown Creeper	BRCR	*Certhia americana*	7.9	4.6	-0.07	13.7	0.13	-4.2	0.29
Common Yellowthroat	COYE	*Geothlypis trichas*	-15.7	-4.9	0.31	-16.8	-0.13	8.4	-0.1
Chestnut-sided Warbler	CSWA	*Dendroica pensylvanica*	-7.1	-1.7	0.19	-17.9	0.09	5.6	-0.11
Least Flycatcher	LEFL	*Empidonax minimus*	3.3	-0.7	-0.03	-25.6	0.27	-1.1	-0.42
Ovenbird	OVEN	*Seiurus aurocapilla*	5.9	0.6	-0.13	-9.8	0.19	-6.1	-0.2
Red-breasted Nuthatch	RBNU	*Sitta canadensis*	6.5	3.6	-0.1	25.1	-0.03	-6.7	0.46
Red-eyed Vireo	REVI	*Vireo olivaceus*	5	0.1	-0.08	-19.7	0.3	-0.2	-0.33
Winter Wren	WIWR	*Troglodytes troglodytes*	0.7	2.3	-0.05	32.3	-0.16	-1.4	0.52
White-throated Sparrow	WTSP	*Zonotrichia albicollis*	-4.2	0.7	0.08	23.2	-0.2	2.3	0.48

†. Values are relative to areas of high versus low habitat quality. For example, the CANOPY value indicates a 13.9 % decrease in canopy closure, and HEIGHT value a 4.1 m decrease in tree height, in areas of the Nipigon Forest that are predicted to have high probability of Alder Flycatcher habitat occupancy, relative to areas of predicted low probability.

Forest Variables

The percentage of hardwoods in the current forest is higher than expected under SRNV, whereas the three management alternatives bring the level of hardwoods closer to that expected under SRNV (Figure 15). Perhaps hardwood levels are currently elevated because of harvest selection for softwoods, or because of failed softwood regeneration efforts. In contrast, the modeled management scenarios all assume perfect regeneration success, and this is probably unrealistic.

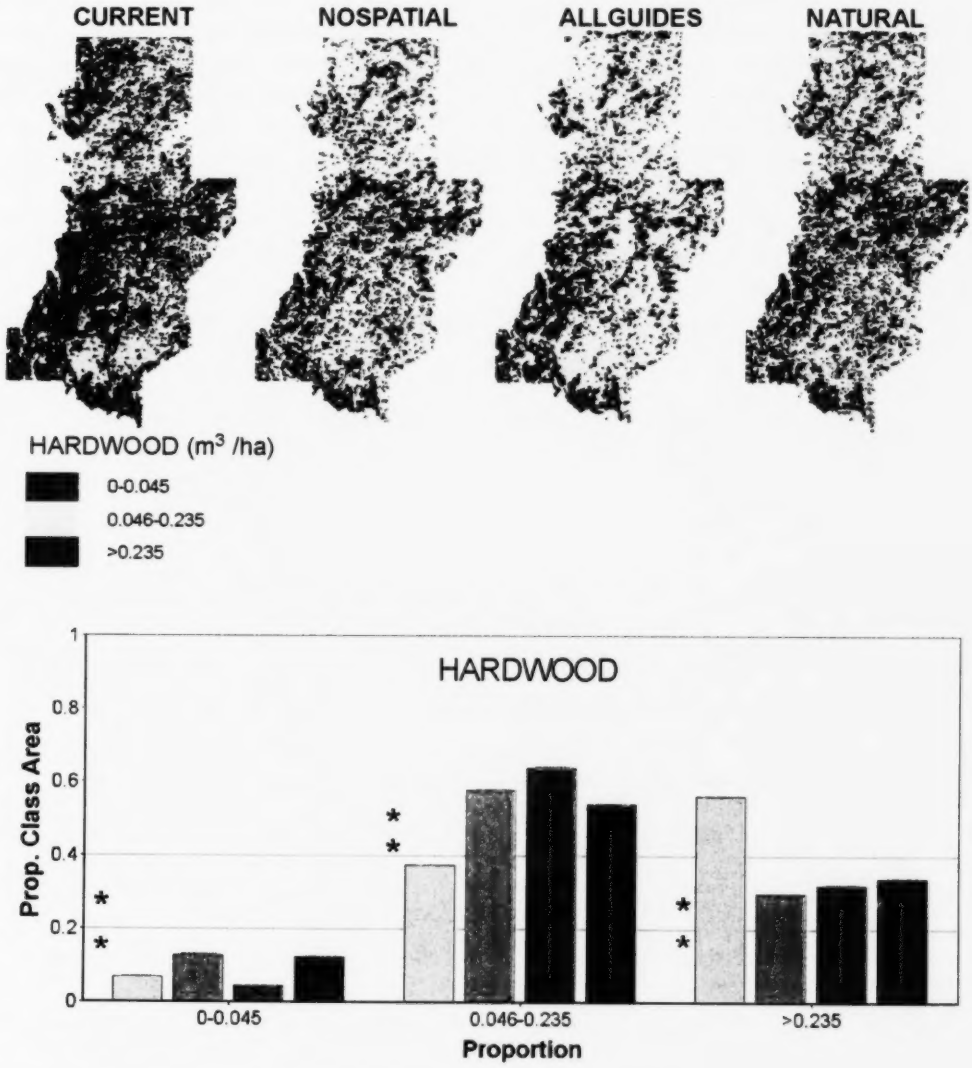
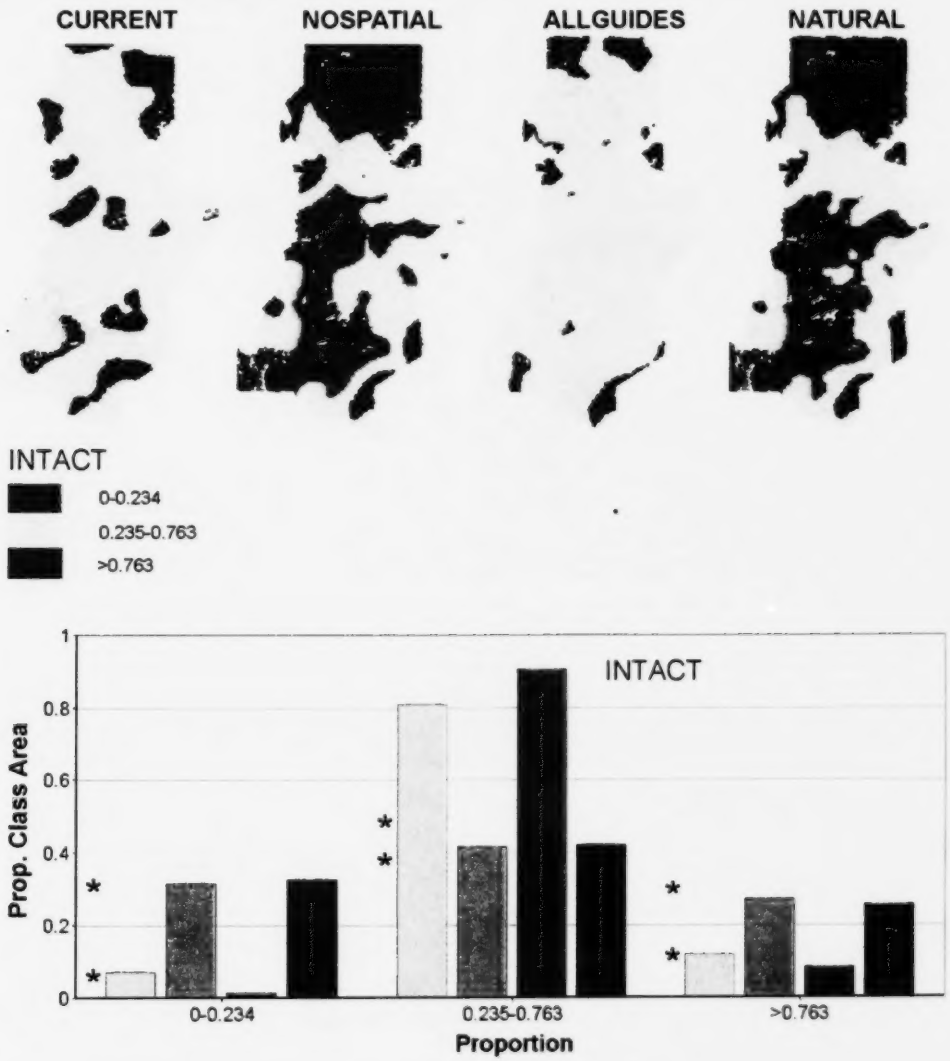


Figure 15. Spatial pattern signatures for percent hardwood volume (HARDWOOD) based on Patchworks projections (year 100) of four management scenarios (see Table 4 for definitions). Histograms depict proportion of map-area for low, medium, and high HARDWOOD for each of the four scenarios, and asterisks represent SRNV for HARDWOOD. Proportions are treated as percentages for discussion.

Maintaining an intact mature forest matrix will be necessary to create habitat for interior forest species, and the forest and management projections based on all featured value management practices have elevated levels of partially fragmented forest matrix. Intermediate levels of intact forest (23.5–76.3 %) were higher in both CURRENT and ALLGUIDES relative to SRNV (Figure 16). In contrast, intact forest matrix is relatively similar to SRNV for both the scenario that provides no landscape-scale spatial direction (NOSPATIAL) and the scenario that prescribes natural composition targets (NATURAL).



Left to right: CURRENT, NOSPATIAL, ALLGUIDES, NATURAL

Figure 16. Spatial pattern signatures for percent mature and old forest (INTACT) based on Patchworks projections (year 100) of four management scenarios (see Table 4 for definitions). Histograms depict proportion of map-area for low, medium, and high INTACT for each of the four scenarios, and asterisks represent SRNV for INTACT. Proportions are treated as percentages for discussion.

At year 100, edge was higher than expected in both the current forest and all three management scenarios. For example, the density of edge between young and old forest is higher than SRNV for all four conditions, but the levels for the highest edge grouping (>12 m/ha) is considerably higher for the ALLGUIDES scenario (Figure 17).

Note, however, that much of the northern part of the Nipigon forest management unit (FMU) became available for harvest in years 80–100 because of caribou-block timings (Figure 12), so the high values of edge in year 100 are a result of the previous 20 years of harvest, and this value should decrease in the subsequent 50 years.

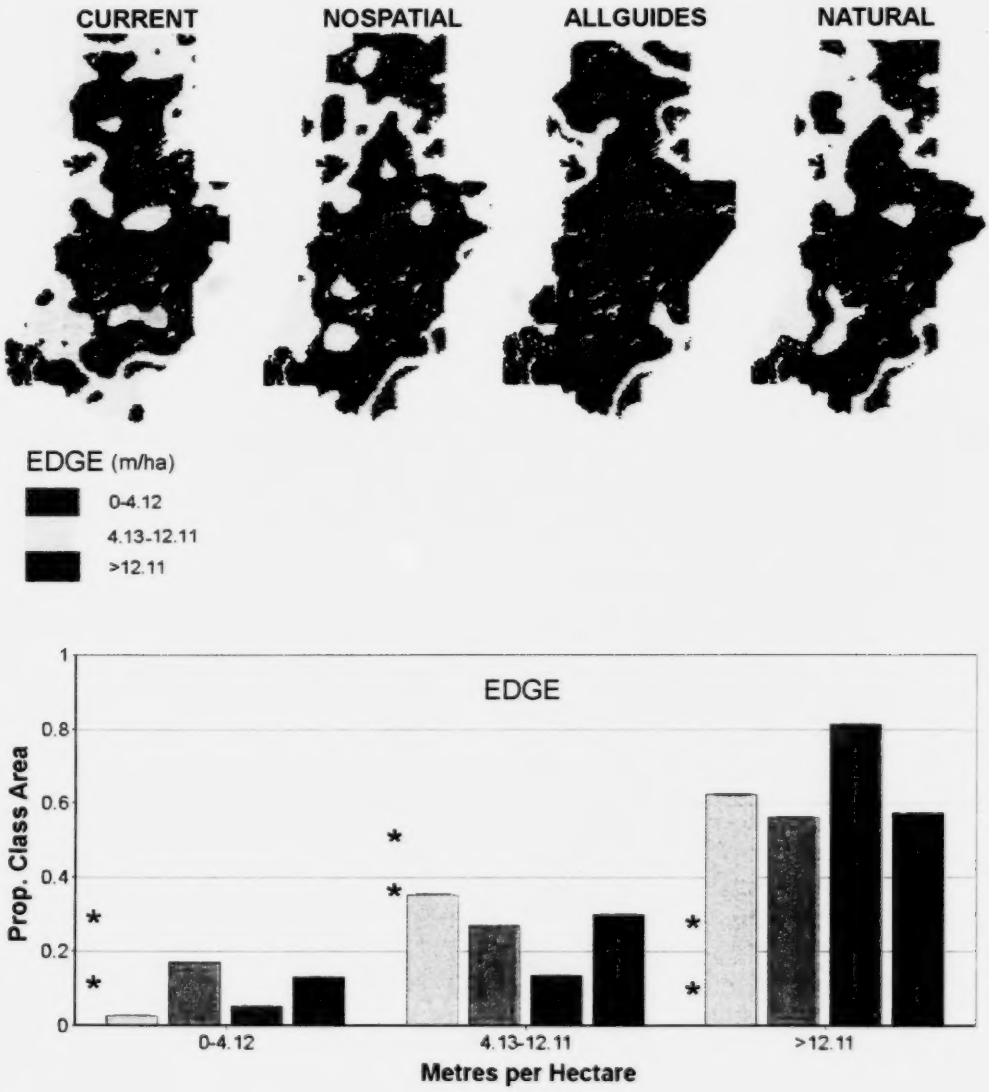


Figure 17. Spatial pattern signatures for contrast weighted edge density (EDGE) based on Patchworks projections (year 100) of four management scenarios (see Table 4 for definitions). Histograms depict proportion of map-area for low, medium, and high EDGE for each of the four scenarios, and asterisks represent SRNV for EDGE.

Scoring the scenarios is based on objectives of the management plan or on policy goals. In this case, the objective is to produce guidelines that will conserve biodiversity through emulation of natural patterns. Consequently, a scenario that causes a forest variable to either increase or decrease from the expected SRNV range was given a -1 score, and those that stayed within the SRNV range were given a score of 1 (Table 6). Overall, at year 100, the scenarios NOSPATIAL and NATURAL produced stand structures and landscape patterns that better stayed within the range of variation for simulated natural patterns. These two scenarios maintained pattern signatures within the bounds of SRNV for the four variables HARDWOOD, CANOPY, AGE, and INTACT, whereas CURRENT and ALLGUIDES maintained pattern signatures within the bounds of SRNV for only one and two variables, respectively (Table 6). Only NOSPATIAL and NATURAL maintained a landscape-scale variable within the bounds of SRNV.

Songbird Habitat

Through the spatial habitat models, forest structure is translated into probabilities of habitat occupancy, and resulting pattern signatures are interpreted similar to the forest signatures. For Black-and-white Warbler, pattern signatures for year 100 demonstrate more habitat for NOSPATIAL and NATURAL compared with ALLGUIDES, relative to SRNV (Figure 18). The habitat model for the early seral stage Black-and-white Warbler (Table 5) translates younger forest, a more fragmented mature forest matrix, and a higher percentage of hardwood forest into highly used habitat.

Spatial and temporal patterns in forest structure are influenced by a number of factors, but for the ALLGUIDES scenario, the caribou mosaic and marten cores (Figure 12) have a pronounced influence, as blocks of forest sequentially become available or unavailable for harvest. For example, the pattern of edge and age over time is influenced by these spatial constraints to harvest, and this is further reflected by the distribution of Winter Wren habitat, which is positively associated with older forest (Figure 19). The sequential timing of these spatial constraints, however, also forces a more even distribution of harvest over the landscape, and over time. This effect can be seen in the distribution of young forest among the three management scenarios, and the patterns of habitat occupancy for species dependent on younger forest (Figure 20).

Table 6. Summary of forest response† relative to simulated range of natural variation (SRNV) for modeled variables at year 0 (CURRENT) and at year 100 (NOSPATIAL, ALLGUIDES, and NATURAL).

Variable	Scenario‡			
	CURRENT †	NOSPATIAL	ALLGUIDES	NATURAL
HEIGHT	1	-1	-1	-1
PHV	-1	1	1	1
PCC	-1	1	1	1
AGE	-1	1	-1	1
PYF	-1	-1	-1	-1
CWED	-1	-1	-1	-1
PMOF	-1	1	-1	1
Sum	-5	1	-3	1

†. Response -1 indicates either an increase or decrease in the overall level of the variable, relative to SRNV, and 1 indicates the variable is maintained within the bounds of SRNV.

‡. Current state of the forest (CURRENT), no spatial guidelines (NOSPATIAL), featured values guidelines (ALLGUIDES), and natural composition targets (NATURAL).

There are clear differences in the temporal patterns for hardwood, intact forest, and Ovenbird habitat among the ALLGUIDES and NATURAL scenarios (Figure 21). Relative to the NATURAL scenario, the ALLGUIDES shows a big drop in the amount of hardwood forest and the amount of mature intact matrix. In contrast, the NATURAL scenario has increasing levels of intact forest over time, and this will provide greater amounts of habitat for interior forest matrix species. Ovenbird shows a decline for both scenarios, in part because of the decrease in hardwood, but the decline is markedly less in the NATURAL scenario.

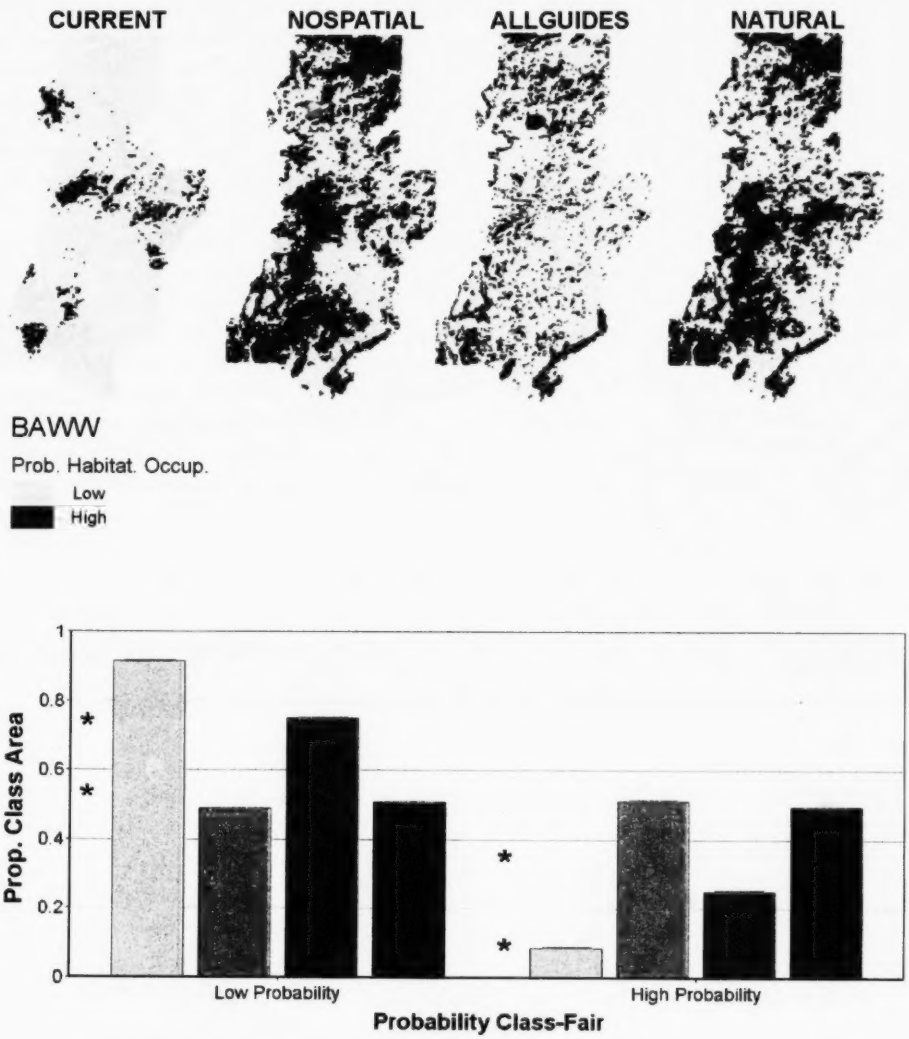


Figure 18. Spatial pattern signatures for Black-and-white Warbler (BAWW) based on Patchworks projections (year 100) of four management scenarios (see Table 4 for definitions). Histograms depict proportion of map-area for low vs. high expected habitat occupancy for each of the four scenarios, and asterisks represent SRNV.

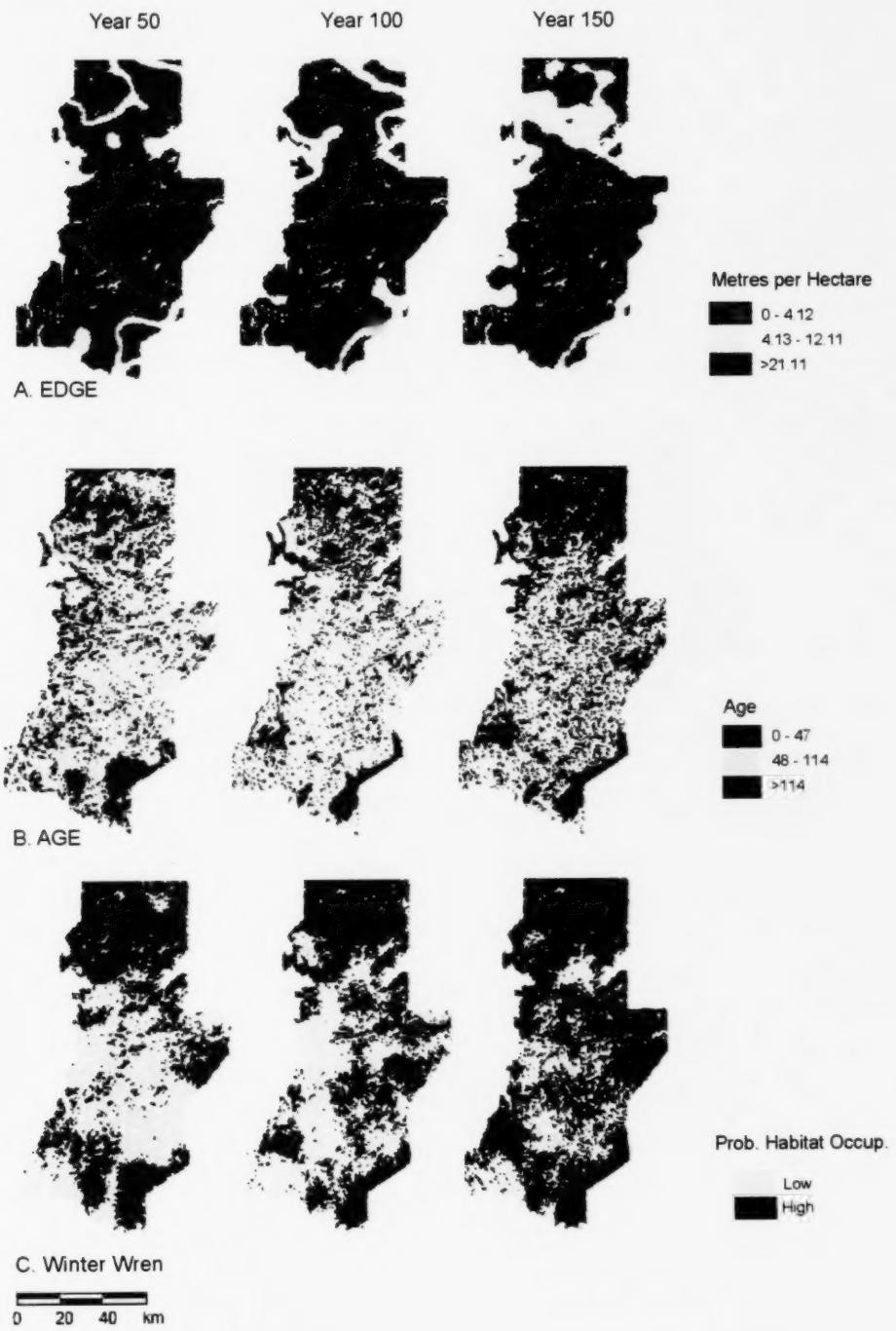


Figure 19. Change in spatial patterns of landscape edge (EDGE), local age (AGE), and predicted habitat occupancy for Winter Wren, under ALLGUIDES scenario for years 50, 100, and 150.

Habitat response was scored slightly different from the forest variable scoring. Where habitat levels decreased below SRNV, the scenario was given a -1 score, but where habitat levels increased above SRNV, the scenario was penalized by a lower value of -0.5. Where habitat was maintained within SRNV, the scenario was scored 1 (Table 7). In addition, the scoring of scenarios was weighted by the accuracy (ROC value) of the habitat model, so models with high discrimination contributed more to the overall score (Table 7).

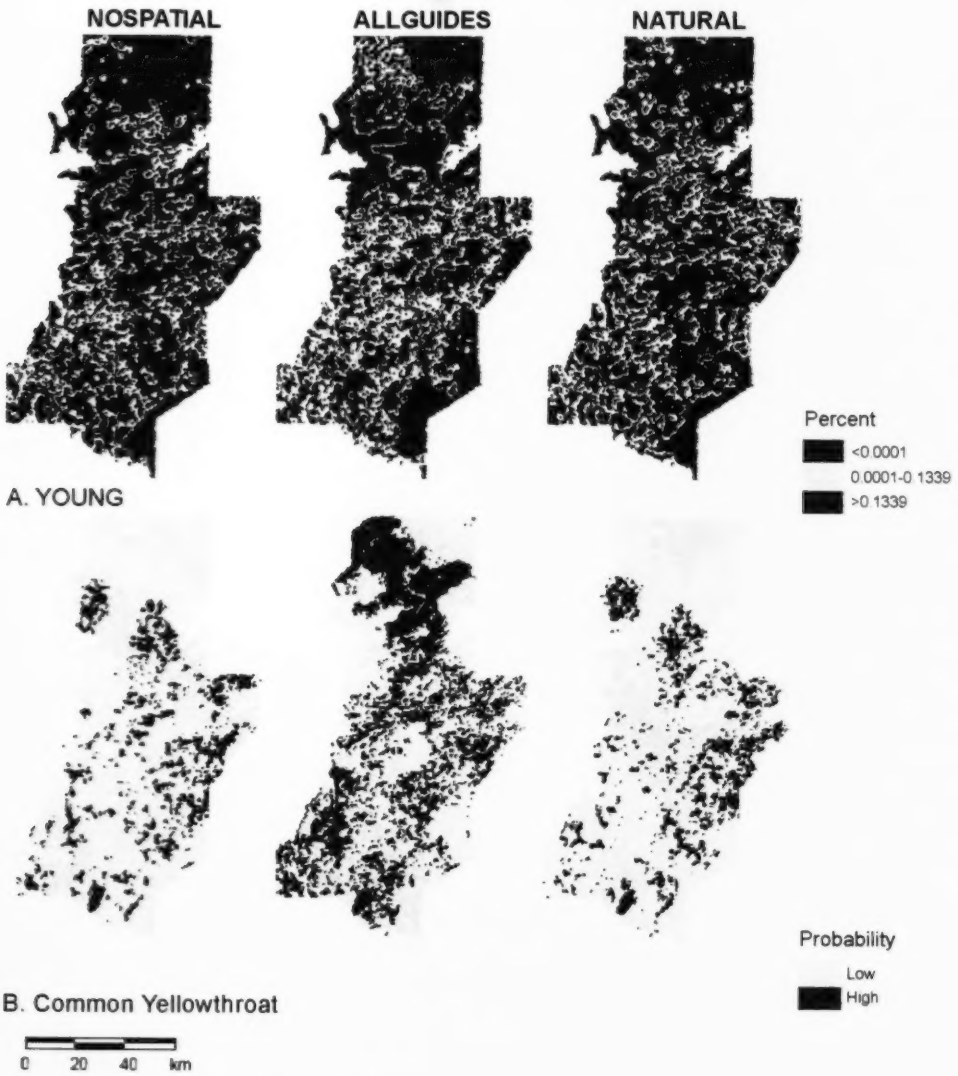


Figure 20. Change in spatial pattern of young forest (YOUNG) at the local scale, and the probability of habitat occupancy for Common Yellowthroat, under scenarios NOSPATIAL, ALLGUIDES, and NATURAL at year 100.

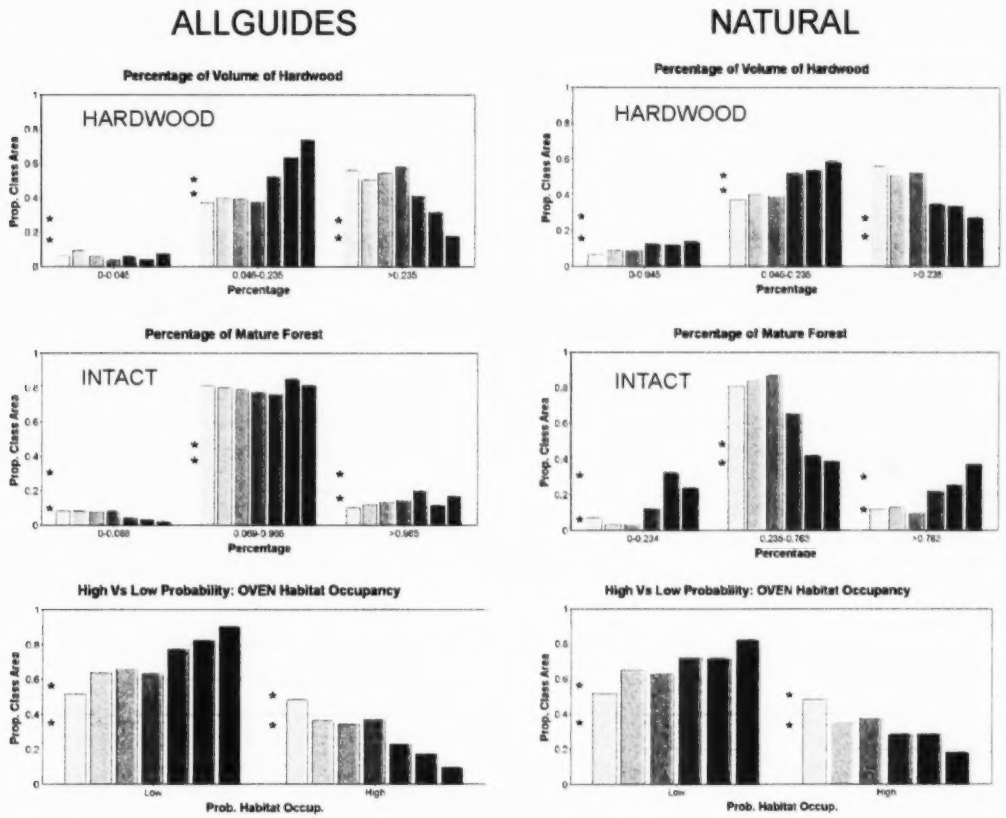


Figure 21. Changes in hardwood (HARDWOOD), intact forest matrix (INTACT), and Ovenbird habitat, for ALLGUIDES and NATURAL scenarios, over years 0, 10, 20, 50, 100, and 150 (light to dark green bars).

Overall, at year 100, habitat levels were maintained within the range of SRNV for six species under NOSPATIAL and NATURAL, whereas only three species were maintained under ALLGUIDES (Table 7). Of the species that prefer lower levels of edge (Bay-breasted Warbler, Blackburnian Warbler, Brown Creeper, Ovenbird, Red-breasted Nuthatch), only Blackburnian Warbler was maintained or increased (relative to SRNV) under the three management scenarios. Five species increased (relative to SRNV) for the ALLGUIDES scenario (Alder Flycatcher, Blackburnian Warbler, Chestnut-sided Warbler, Red-eyed Vireo, and White-throated Sparrow), and four of these are associated with either younger forest or higher levels of local disturbance. In terms of overall score, the CURRENT scenario performed just slightly better than the NOSPATIAL or NATURAL scenario, and the ALLGUIDES had a substantially lower score (Table 7).

Discussion

The distribution of natural wildfires is contagious, resulting in landscapes with clustered areas of high edge separated by large areas with low edge (Rowe and Scotter 1973). It is not surprising, then, that a community of species as diverse as the forest songbirds will exhibit a variety of species-specific responses to edge (Wedeles and Donnelly 2004, Parker et al. 2005, Schieck and Song 2006). Maintaining the assemblage of forest songbirds, as represented by the focal species group, requires maintenance of habitat conditions that favour hardwood vs. softwood species, old forest vs. young forest species, and edge-loving vs. edge-avoiding species. In this study, the focus of assessing resilience was from a community perspective, and this was achieved by selecting a focal group of species representing a broad range of habitat needs (Rempel 2007). Evaluating forest

Table 7. Summary of habitat response† relative to simulated range of natural variation (SRNV) for modeled variables at year 0 (CURRENT) and at year 100 (NOSPATIAL, ALLGUIDES, and NATURAL).

Species	Scenario‡				ROC
	CURRENT	NOSPATIAL	ALLGUIDES	NATURAL	
Alder Flycatcher	1	1	-0.5	1	0.77
Black-and-white Warbler	-1	-0.5	1	-0.5	0.678
Bay-breasted Warbler	-1	-1	-1	-1	0.725
Blackburnian Warbler	-0.5	1	-0.5	1	0.668
Brown Creeper	-0.5	-1	-1	-1	0.728
Common Yellow-throat	-1	-1	-1	-1	0.833
Chestnut-sided Warbler	-0.5	1	-0.5	1	0.757
Least Flycatcher	1	1	1	1	0.687
Ovenbird	1	-1	-1	-1	0.796
Red-breasted Nuthatch	1	-1	-1	-1	0.708
Red-eyed Vireo	-0.5	-0.5	-0.5	-0.5	0.803
Winter Wren	1	1	1	1	0.809
White-throated Sparrow	1	1	-0.5	1	0.749
Sum	1	0	-4.5	0	
Weighted Sum§	0.8	-0.09	-3.49	-0.09	

†. Response - 0.5 indicates an increase in the overall level of the variable, relative to SRNV, and -1 represents a decrease. 1 indicates the variable is maintained within the bounds of SRNV.
‡. Current state of the forest (CURRENT), no spatial guidelines (NOSPATIAL), featured values guidelines (ALLGUIDES), and natural composition targets (NATURAL).
§. Sum weighted by ROC model accuracy.

management policies and practices in terms of this complex assemblage is almost impossible without the use of spatial habitat models that can translate alternative forest configurations into probabilities of habitat occupancy for individual species, over space and time.

Creating the complex arrangement of habitat conditions to support the songbird community requires an understanding of how the distribution and abundance of habitat components relate to the distribution and abundance of the individual focal species. The spatially explicit, multiple-scale habitat models applied here help achieve this understanding, and when applied to forest harvest and succession models, provide the facility to project the expected outcomes of alternative forest harvesting strategies that alter landscape pattern. Interpreting the relative success of the scenarios in terms of conservation management objectives is assisted by positioning these projections in the context of natural disturbance processes (i.e.,SRNV). In our assessment of the three management scenarios, some interesting perspectives emerged. It appears that the greater the number of value-specific landscape-scale rules that are in place (e.g., the ALLGUIDES scenario), the less similar the resulting landscape is to that expected under SRNV. Rules that dictate the creation of the artificial patterns, such as shoreline forest reserves (fish habitat guidelines) and dispersed block cuts (moose guidelines) force the arrangement of mature forest into linear strips and isolated patches. Therefore, it is not surprising that this deviation from natural patterns has predicted negative consequences on biodiversity objectives, especially when a full array of disturbance-preferring and disturbance-avoiding species is considered. In contrast to the scenario that does not prescribe any landscape-scale direction (NOSPATIAL), ALLGUIDES again performs poorly for some species. This finding is not new.

For example, Loehle et al. (2002, 2006) found in their spatial assessment of forestry guidelines that block-size restriction and riparian buffer strips were both expensive and of little value to songbirds. If the principal objective is to emulate natural patterns (OMNR 2002), then the current set of spatial guidelines used in Ontario performs poorly. This is almost certainly related to the large number of small clearcuts and linear buffer strips that are spread evenly across the landscape.

The ALLGUIDES scenario, however, also explicitly defines broad spatial and temporal patterns based on timings for availability with caribou blocks and marten core area reserves (Figure 12), and the ALLGUIDES includes non-spatial old-growth targets and spatial pattern objectives based on the Natural Pattern Emulation Guidelines (OMNR 2002). This scenario results in positive aspects for biodiversity conservation, including the maintenance of relatively large patches of mature forest throughout the forest management unit, over time, and is reflected in the patterns of predicted habitat occupancy for Winter Wren (Figure 19). As well, it may be necessary to deviate from natural patterns to achieve social objectives. Ontario's Crown Forest Sustainability Act directs forest management to emulate natural disturbance landscape patterns, within the limits of silviculture, while minimizing the negative effects on a range of social, economic, and ecological values (Government of Ontario 1994). For example, linear strips of forest along canoe routes provide excellent wilderness experience conditions, so, from a human–habitat perspective, it is important to maintain at least some of these linear strips of old forest. In contrast, maintaining artificially high levels of older coniferous forest in narrow strips along such water bodies reduces the suitability for beaver habitat (Martell et al. 2006). This may have cascading biodiversity and ecosystem resilience consequences, especially for waterfowl populations occupying active beaver ponds, and other species requiring the wet meadows created by abandoned ponds. The final selection of policy options for management guides or the preferred management option for forest management plans will depend on a number of factors. The role of spatial habitat and forest simulation models is simply to help inform decision making, and to help place management objectives and decisions in a broader context of ecosystem resilience and biodiversity conservation.

Composition target objectives (e.g., retained abundance of mature mixedwood) for the NATURAL scenario were based on the results from initial runs of the BFOLDS, so it is by design that the NATURAL scenario more closely resembles the SRNV. Thus, BFOLDS-based SRNV provides both a baseline context for evaluating changes in forest structure and habitat occupancy patterns, and the composition targets for the natural pattern scenario in Patchworks. This begs the question of accuracy and bias of the disturbance simulator and succession curves. The BFOLDS is based on published research findings for component processes, such as stand succession and rates of fire spread (Perera et al. 2004), and simulation models are the only reasonable way we can estimate the range of conditions expected under a pristine natural disturbance regime. Theoretical comparisons have shown that BFOLDS fire-spread rates, fire intensities, and sizes of fire events are comparable to theoretical predictions under most weather conditions (Cui and Perera, in review). The predictions of generally lower edge at the eco-regional level under a natural disturbance regime make intuitive sense, and are supported by observations of regions in the far north of Ontario, where fire suppression does not occur.

There are clear limitations and qualifications to projecting 100 or even 5 years into the future, however, several key spatial/temporal policy options in the Nipigon Forest (e.g., the caribou mosaic deferment blocks) require simulation of at least 100 years, as some blocks only become available at year 80 (Figure 12). The spatial harvest model for the Lake Nipigon Forest was based in part on transportation networks and location of mills, but two paper mills closed and one plywood mill burned within 1 year of running the model. Thus, even a simulation period of only 5 years is too long in terms of model realism. Climate change, political trends, and economic volatility will certainly add additional uncertainty, and a host of environmental factors (including windthrow, wildfire, and insect outbreaks) will ultimately invalidate any specific predictions. The models are based on the simplifying assumption that certain environmental, political, and economic factors are held constant, whereas other exploratory factors are varied. The models are meant to provide strategic and general insights within a framework of operational realism, but the application of the models (as used in this

study) cannot accurately predict exactly what will happen on any given piece of ground at any future given time. In contrast, it might be useful to vary climatic factors, while holding a few management options constant, and this will be the focus of future research.

The meta-modelling approach used in this study introduces several key elements of model uncertainty. Among the natural disturbance simulation, spatial habitat, harvest schedule, stand succession, and canopy closure models, a key model in this study is the spatial habitat model. The spatial habitat models are based on data collected using a mensurative design, where patterns of association are derived from empirical songbird observations using existing combinations of factors in the field. The mensurative approach permits extensive sampling over large areas, and this is important to reduce the influence of spatial-autocorrelation with landscape-scale variables, but compared with a controlled experimental design, the mensurative approach reduces the ability to statistically control for environmental variability. As well, the empirical models do not demonstrate cause and effect or estimate relative fitness within habitat types—they only establish patterns of association—and in many cases, it is still unknown why a species would select areas of high edge. Perhaps these areas have higher densities of food items such as flying insects or seeds (Parker et al. 2005), but the explanations are still generally unknown and require further research.

Focal species were selected to represent the entire forest songbird community, and the species selected for the focal group essentially represent the extreme conditions within the community niche-space. For example, species with the strongest need for an intact mature forest matrix, the greatest need for high edge, or strongly selecting closed hardwood, were included in the focal group. Modelling habitat conditions for this focal group provides solid information to help forest managers develop and evaluate plans that will create a sufficient range and diversity of forest conditions to support the songbird community. However, the variables considered in this study should be considered coarse-filter variables, and thus, the spatial habitat models simply describe the general framework of forest structure and pattern required by the focal species. Scenario evaluation is partly dependent upon the accuracy of the habitat models, so models should be continuously tested and updated in an adaptive management context, with the goal of better understanding cause–effect relationships.

The scale at which variables were measured was partly arbitrary, in that the 50-ha scale was selected for local-scale variables because it corresponds to the extent of area surveyed by a cluster of listening point stations, and the 5000-ha scale was selected for landscape-scale effects because this corresponds to the maximum distance of spatial autocorrelation generally found between listening stations, and is in the approximate size of many stand-structuring wildfire events. For a community-level study, it was useful to standardize the scale of measurement to facilitate comparisons among species. However, further exploration of the inter-correlation of variables measured at differing scales, and the correlation of these variables with habitat occupancy may lead to more precise habitat models.

CONCLUSIONS

To be successful, biodiversity conservation strategies must emulate the patterns created through natural disturbance by maintaining the full range of forest cover homogeneity and heterogeneity on the landscape. This variation in landscape pattern can be achieved by creating habitat conditions to support a range of focal species that collectively describe the wide range of niche-space occupied by the forest songbird community. The combination of community-level and species-level analyses help to identify the set of focal species that land managers should consider when developing forest management plans. Providing the habitat needs for all members within this focal group will ensure important "coarse-scale" habitat needs are not lost on the landscape. Defining the habitat needs for individual species within the focal group provides the basis of a concrete strategy for identifying appropriate levels and combinations of landscape patterns required to conserve biodiversity for a broad range of forest songbirds, and perhaps even the invertebrates and other food-web species associated with these birds. Future studies need to evaluate these predications at different times

and places because habitat associations may be influenced by as yet unidentified causal factors (e.g., distributions in insect prey abundance). Although many of the local-scale habitat associations are relatively well known, most of the landscape-scale habitat associations are less well understood. Further study is required to evaluate the robustness of habitat associations at the broader landscape scales.

The results of this study support the adoption of boreal forest management strategies that create clustered areas of high edge separated by large areas of intact forest matrix. It is the combination of these conditions that will create the diversity of forest patterns necessary to support the full range of boreal forest songbirds. The analysis also supports using compositional targets based on natural disturbance simulations. At the community level, some songbird species are resilient to edge, and others less so. Only by creating the combination of conditions will the coarse-filter habitat needs of the entire community be met. Spatial habitat models developed for a focal set of songbird species describe the target levels and range of variability in forest conditions required, as a minimum, to support the full complement of boreal forest songbird species. The simulated range of natural variability helps define the temporal variability that should be expected for both forest variables and associated habitat occupancy patterns. The approach of strategically modelling long-term patterns, but using realistic constraints adds both validity and complexity to model interpretation.

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ISBN 978-1-4249-5174-1
(0.05k P.R. 24 09 07)